Musculature and Nervous System of the Thorax, of the Sound Mechanism, and of a Typical Pregenital Abdominal Segment of the Male of the Annual Cicada, *Tibicen chloromera* (Walker) (Homoptera: Cicadidae)[1]

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Abstract: The musculature and innervation of the thorax, sound mechanism, and the fourth abdominal segment of the male annual cicada, *Tibicen chloromera* (Walker) are described.

The ventral nerve cord consists of a subesophageal ganglion, prothoracic ganglion, and a thoracic–abdominal ganglionic mass. There are no ganglia present in any of the abdominal segments. The prothoracic ganglion supplies innervation to some of the muscles of the cervical area and the muscles of the prothorax. The thoracic–abdominal ganglionic mass provides innervation to the posterior tergo-sternal muscles of the prothorax, the muscles of the prothorax, the muscles of the mesothorax, metathorax, and all of the abdominal segments. The abdominal segments are innervated by lateral nerve branches which arise from a pair of nerves that originate from the posterior portion of the thoracic–abdominal ganglionic mass located in the mesothorax. No median nerves are visible between the subesophageal ganglion, prothoracic ganglion, and the thoracic–abdominal ganglionic mass. The median nerves are probably included within the interganglionic connectives.

The members of the family Cicadidae are among the largest insects classified in the order Homoptera. Their periodic occurrences in large numbers and the shrill "song" produced by the males have probably aroused the curiosity of man since the beginning of time. Despite their large size and the interest they have received by virtue of their sound-producing apparatus, cicadas have been somewhat neglected by morphologists. This study was undertaken as a contribution to our knowledge of the musculature and innervation of the thorax, of the sound mechanism, and of a typical pregenital abdominal segment of the male of the annual cicada, *Tibicen chloromera* (Walker).

A study of the nerve patterns in insects may be approached with at least two different objectives in mind. From a physiological or histological standpoint, a knowledge of nerve and muscle arrangements is a necessary prerequisite for precise investigations. From a morphological standpoint, a knowledge of the hexapod nervous system is essential in establishing nerve and muscle homologies and thereby provide additional information on the course of phylogenetic development. This paper is an attempt in the latter direction with the full understanding that detailed investigations of many more forms are necessary in order to establish the course of phylogenetic development.

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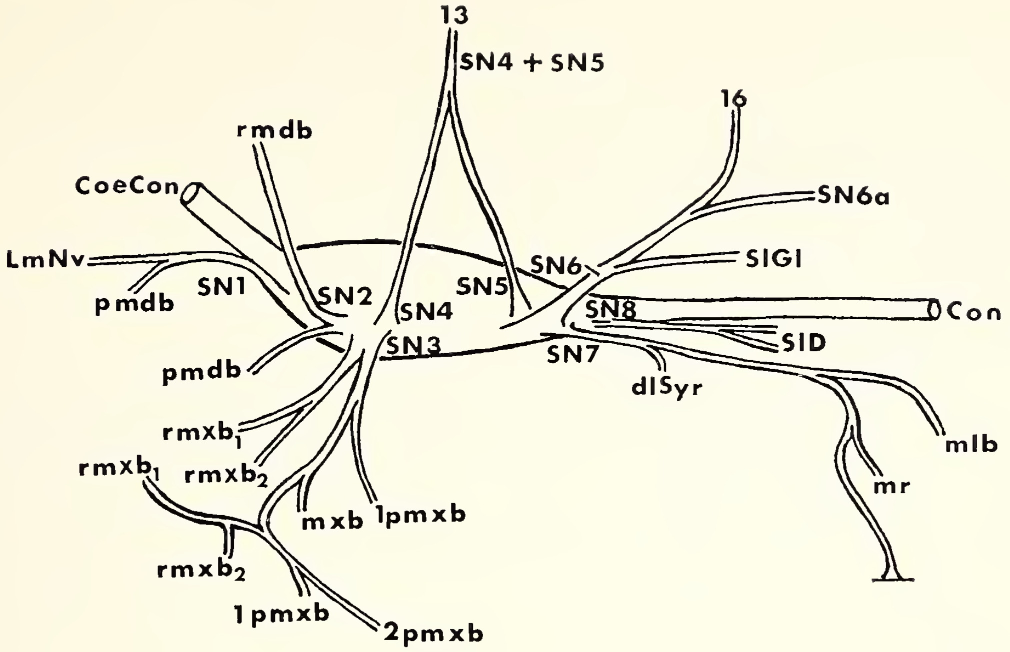

Figure 1A

Fig. 1A. Lateral view of the subesophageal ganglion of the male annual cicada *Tibicen chloromera* (Walker).

The concept of an underlying homology of segmental musculature has provided important evidence on the evolution of the insect thorax and appendages. This concept is based on the assumption that at sometime in the past history of the Hexapoda, the abdominal somites, as leg-bearing segments, had essentially the same structure as the primitive thoracic and gnathal segments. If we assume that the innervation pattern as well as the musculature was homologous in each ancestral segment then the nerve configuration manifested in insects today is a variation of the ancestral pattern. Moreover, since the inherent purpose of the nervous system is to transmit nerve impulses, selective pressure on the nerve pattern would be less than on the structures innervated (Schmitt, 1959). This assumption should not be interpreted to imply that the nervous systems of insects have remained static in the course of phylogenetic development, but rather that through investigations of the segmental innervation patterns of insects and by establishing criteria of homology of nerves through the utilization of primitive muscle groups and nerve junctions, a knowledge of the course of the phylogenetic development of the nervous system should be possible.

Unfortunately, only a very few comparative morphological investigations have been presented in the literature concerning the establishment of nerve homologies in insects. The writer hopes that this paper will be a significant addition to the existing studies and serve to cultivate further interest regarding the concept of a basic plan of segmental innervation.

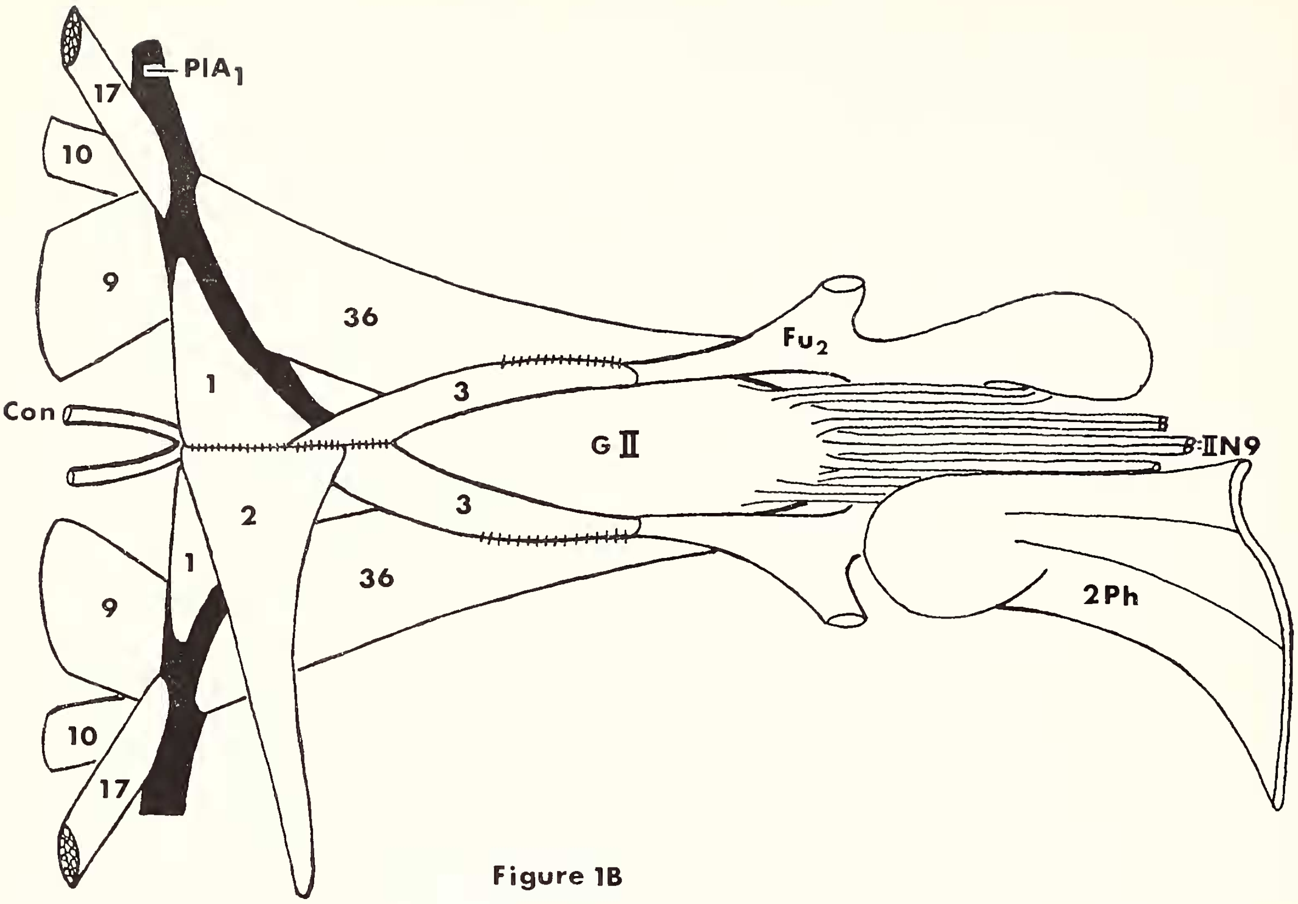

Figure 1B

Fig. 1B. Dorsal view of ventral muscles that cover the prothoracic ganglion and anterior portion of the thoracic–abdominal ganglionic mass of the male annual cicada *Tibicen chloromera* (Walker).

OBJECTIVES

1. Determine the musculature of the thorax of the male of the annual cicada, *Tibicen chloromera* (Walker) and compare this musculature to that of *Huechys sanguinea* var. *philaemata* as described by Maki (1938) and to that of *Cicada* (= *Tibicen*) *plebeia* as described by Berlese (1909).
2. Describe the ventral nerve cord of *Tibicen* and compare its configuration to the ventral nerve cords previously described in the family Cicadidae.
3. Determine and describe the cervicothoracic nervous system of the male of *Tibicen chloromera* (Walker) and, if feasible, to establish criteria of homology.
4. Determine the musculature of the first abdominal segment of *Tibicen* which contains the sound mechanism and compare this musculature to that described by Maki (1938) for *Huechys* and to that of *Cicada* (= *Tibicen*) *plebeia* as described by Berlese (1909).
5. Determine the innervation of the first abdominal segment of the male of *Tibicen chloromera* (Walker).
6. Determine the musculature of a typical pregenital abdominal segment of

Table 1. Ventral muscles covering the prothoracic and thoracic–abdominal ganglia of *Tibicen chloromera* (Walker).

Muscle number	Origin	Insertion
1	Pleural arm of prothorax	Zygomatic with muscles 2 and 3 over the prothoracic ganglion and the anterior portion of thoracic–abdominal ganglionic mass.
2	Anterior margin of episternum ventral to tergo-pleural 40	Zygomatic with muscles 1 and 3 over the prothoracic ganglion and the anterior portion of thoracic–abdominal ganglionic mass.
3	Anterior mesofurcal arm	Zygomatic with muscles 1 and 2 over the prothoracic ganglion and the anterior portion of thoracic–abdominal ganglionic mass.

Tibicen and compare this musculature to that described by Maki (1938) for *Huechys.*

7. Determine the innervation of a typical pregenital abdominal segment of *Tibicen* and, if feasible, to establish criteria of homology.

REVIEW OF LITERATURE

The literature will be reviewed under five major headings corresponding to their order of presentation in this paper.

1. THE VENTRAL NERVE CORD

Comparatively little is known concerning the general nerve configuration in the families of the order Homoptera. The principal writers reporting on the ventral nerve cord of cicadas are: Binet (1894), Dufour (1833), Hilton (1939), and Myers (1928). It may be stated that within the family Cicadidae a high degree of specialization has taken place as far as the nervous system is concerned (Myers, 1928). The chief evidence of this specialization is the fact that all abdominal ganglia have become consolidated within the large thoracic–abdominal ganglionic mass located in the mesothorax.

Binet (1894) described the subintestinal nervous system of *Cicada orni.* By microscopic sections of the thoracic–abdominal ganglionic mass, Binet was able to distinguish the abdominal ganglia by the absence of crural lobes correlated with the absence of legs in corresponding segments (Myers, 1928).

Dufour (1833), in an earlier publication, described the ventral nerve cord in *Cicada orni* as having a cephalic ganglion and two thoracic ganglia. The thoracic ganglia are nearly fused, forming one oblong body which is covered dorsally by a mass of muscles which occupy the lower wall of the thorax. Dufour states that the anterior thoracic ganglion gives rise to four pairs of principal nerves, while the posterior ganglion gives rise to six pairs of nerves. The nerve cords

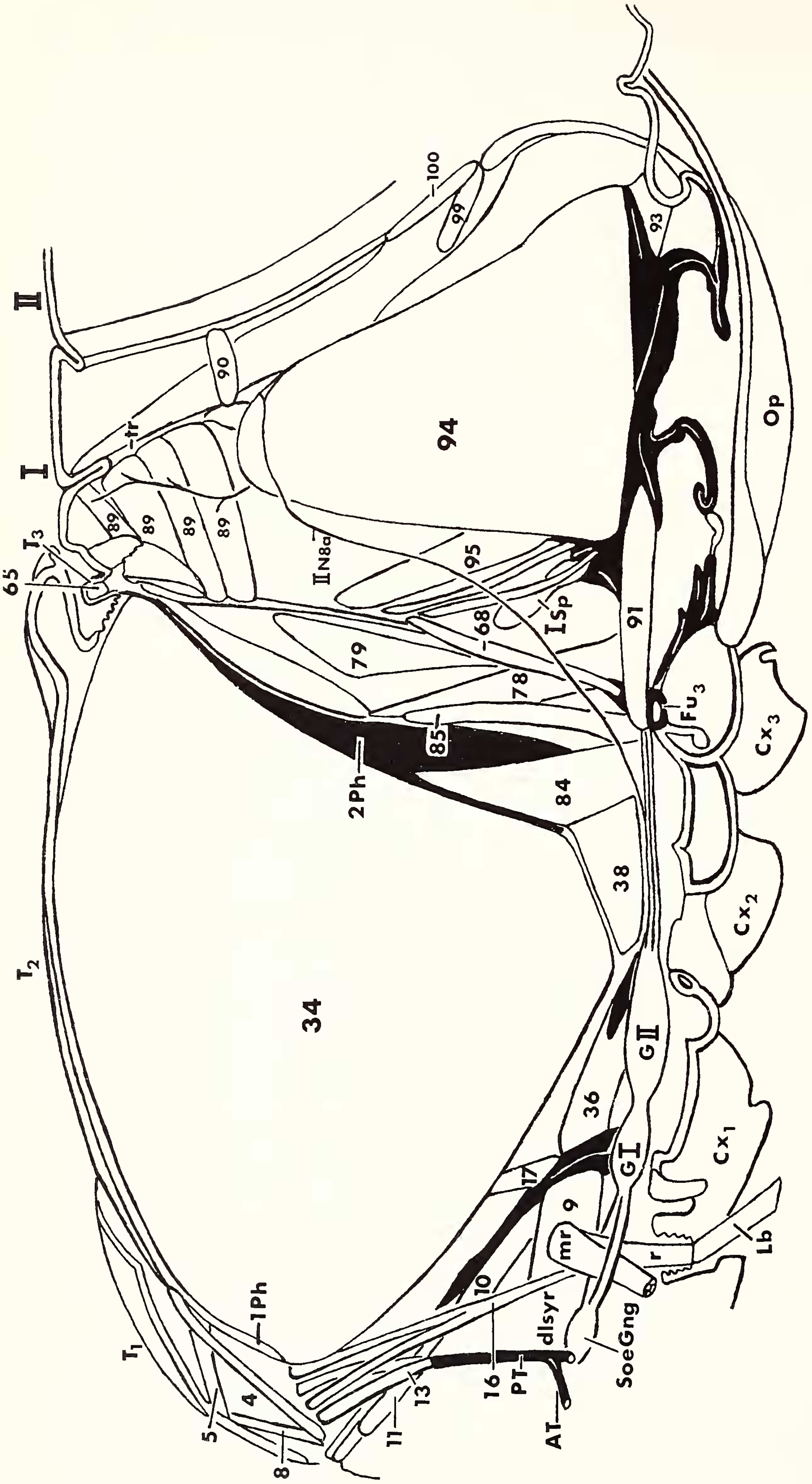

FIG. 2. First stage dissection showing muscles of the cervix, thorax, and first abdominal segment and the ventral nerve cord in longitudinal section in the male annual cicada *Tibicen chloromera* (Walker).

which innervate the abdominal segments are adherent at their origin but separate before finally dividing in the abdominal cavity. Dufour did not describe the subesophageal ganglion which, according to Myers (1928), may have been mistaken for the brain.

Hilton (1939) described the central nervous system for both the immature and adult stages of a cicada. Unfortunately, no mention is made of the species studied. There were two ganglia in both the immature and mature cicada other than the superesophageal ganglion. Hilton further stated that there are many large, long nerves issuing from the caudal portion of the large thoracic–abdominal ganglion.

Myers (1928) described the brain and ventral nerve cord of *Melampsalta sericea.* The round subesophageal ganglion is connected to the first ganglionic mass by a pair of long, stout, well-separated interganglionic connectives. The first ganglionic mass lies largely in the prothorax. Two short, very stout interganglionic connectives join the first ganglionic mass to the second thoracic mass which lies wholly within the mesothorax. Myers states that the second thoracic mass is much longer than broad and displays signs of a two fold origin. However, from the standpoint of gross anatomy, the abdominal ganglia cannot be distinguished. Nerves that innervate typical abdominal segments superficially appear to arise as a single cord as they leave the second thoracic mass. Later the single cord splits into two nerves as it enters the abdomen.

2. THORACIC MUSCULATURE

The thoracic musculature of two species of cicadas have been described by Berlese (1909) and Maki (1938). Berlese (1909) described in some detail the thoracic musculature of *Cicada* (=*Tibicen*) *plebeia.* Muscles are identified in figures by Roman or Arabic numerals while descriptions of muscle origins and insertions are included in the text. An attempt is made to homologize the thoracic musculature of several species of insects. Unfortunately, with respect to *Cicada* (= *Tibicen*) *plebeia,* it appears many of the muscles that originate on the furcal and pleural arms and attach to the coxae and trochantine are omitted.

Maki (1938) presents a very detailed description of the thoracic muscles of *Huechys sanguinea* var. *philaemata.* Muscles are identified by their position and function; however, in tables and figures, Arabic numerals are utilized for muscle numbers. Muscle origins and insertions are described in the text.

In his study of Hemiptera, Maki presents the thoracic musculature of *Eurostus validus, Sigara substriata, Cicadella ferruginea, Macrohomotoma gladiatum,* and *Huechys sanguinea* var. *philaemata.* Maki includes in his tables the musculature of *Nezara viridula* by Malouf (1933), *Cicada plebeia* by Berlese (1909), and *Psylla mali* by Weber (1929).

Snodgrass (1927 and 1935), illustrates a portion of the thoracic musculature of *Tibicina* (= *Magicicada*) *septendecim* as an example of indirect wing muscles.

TABLE 2. Prothoracic musculature of *Tibicen chloromera* (Walker).

Muscle	Muscle number	Origin (or attachment)	Insertion (or attachment)
Dorsal muscles			
Median dorsal	4	Posterior edge of head	First phragma
Median dorsal	5	Dorsolaterally on middle of tergum	First phragma
Lateral dorsal	6	Dorsolaterally on middle of tergum	Anterolateral region of first phragma
Lateral dorsal	7	Dorsolaterally on middle of tergum	Anterior edge of first phragma
Anterior dorsal	8	Posterior edge of head	Dorsolateral midportion of tergum
Ventral muscles			
Internal ventral	9	Posterior tentorial arm	Sternal apophyses
External ventral	10	Posterior end of cervical sclerite	Pleural arm of prothorax
Tergo-sternal muscles			
Anterior intersegmental	11	Posterior edge of head	Ventrolateral cervical sclerite
Anterior intersegmental	12	Posterior edge of head	Ventrolateral cervical sclerite
Anterior intersegmental	13	Anterior dorsolateral region of tergum	Posterior tentorial arm
Anterior intersegmental	14	Dorsolateral region of tergum	Posterior tentorial arm
Anterior intersegmental	15	Anterior dorsolateral region of tergum	Ventrolateral cervical sclerite
Anterior intersegmental	16	Dorsolateral region of tergum	Base of tentorium
Posterior tergo-sternal	17	Anterolateral portion of mesotergum	Pleural arm of prothorax
Tergo-pleural muscles			
Anterior tergo-pleural	18	Dorsolateral portion of posterior edge of head	Base of prothoracic pleural arm
Anterior tergo-pleural	19	Dorsolateral portion of posterior edge of head	Base of prothoracic pleural arm
Ordinary tergo-pleural	20	Middle of lateral region of tergum	Pleural arm of prothorax
Coxal muscles			
Tergal promotor	21	Dorsolateral region of tergum	Anterior rim of coxa
Tergal promotor	22	Lateral region of tergum	Apodeme of trochantin
Sternal promotor	23	Profurca	Anterior basal rim of coxa
Tergal remotor	24	Middle dorsolateral region of tergum	Remotor apodeme of coxa
Tergal remotor	25	Oblique ridge at middle of lateral region of tergum	Remotor apodeme of coxa
Tergal remotor	26	Tergum external to 25	Posterior basal rim of coxa
Tergal remotor	27	Lateral region of tergum beneath 26	Posterior basal rim of coxa
Sternal remotor	28	Profurca	Posterior basal rim of coxa
Tergal abductor	29	Midportion of dorsolateral region of tergum	Apodeme anterolateral basal rim of coxa
Pleural abductor	30	Pleural arm of prothorax	Anterior basal rim of coxa
Pleural abductor	31	Pleural arm of prothorax	Anterior basal rim of coxa
Trochanteral muscles			
Tergal depressor	32	Midlateral region of tergum	Depressor apodeme of trochanter
Pleural depressor	33	Pleural arm of prothorax	Depressor apodeme of trochanter

The muscles illustrated in the mesothorax are the longitudinal dorsal, oblique dorsal, anterior tergo-sternal, and posterior tergo-sternal. The metathoracic depressor muscles of the trochanter and the coxal part of the depressor muscle of the trochanter are also included.

The above muscles are homologous to those of *Cicada* (= *Tibicen*) *plebeia* (Berlese, 1909), *Huechys sanguinea* var. *philaemata* (Maki, 1938), and *Tibicen chloromera* with respect to their origins and insertions.

3. THE CERVICOTHORACIC NERVOUS SYSTEM

Detailed descriptions of the thoracic nervous system have not appeared in the literature for any member of the family Cicadidae nor for any insect in the order Homoptera. Moreover, the literature contains only a relatively few studies regarding the thoracic nervous systems of insects. One reason for this lack of information is due to the time-consuming nature and patience necessary for such research. Therefore, the majority of nerve studies have been restricted to anatomical facts and descriptions of nerve cord configurations. The principal writers who have contributed detailed information on thoracic nervous systems of insects are: Holste (1910) on *Dytiscus marginalis*, Johansson (1957) on *Oncopeltus fasciatus*, Maki (1936) on *Chauliodes formosanus*, Marquardt (1939) on *Carausius morosus*, Matsuda (1956) on *Agulla adnixa* and *Blattella germanica*, Nüesch (1957) on *Telea polyphemus*, Pipa and Cook (1959) on *Periplaneta americana*, Schmitt (1959) on *Dissosteira carolina*, and Wittig (1955) on *Perla abdominalis*.

Schmitt (1962) states that an additional reason for the lag of nerve topography studies in insects is due to the difficulty in relating the findings on one group to those on another group. Furthermore, Maki (1936) and Pipa and Cook (1959) state that there exists a remarkable degree of variability in nerve distribution patterns of different individuals of the same insect species. However, Pipa and Cook (1959) also state that the existence of a fundamental plan in the peripheral distribution of thoracic nerves in widely separated insects is evident. Wittig (1955) describes the innervation pattern in the thorax of the larva and adult of *Perla abdominalis*. She presents a comparison of the innervation fields of the thoracic nerves of *Perla abdominalis* with those of *Chauliodes formosanus* as reported by Maki (1936), *Carausius morosus* as reported by Marquardt (1939), and *Dytiscus marginalis* as reported by Holste (1910) and establishes the existence of nerve homologies in these widely separated insects.

Pipa and Cook (1959) state that the pattern of nerve distribution in *Periplaneta americana* essentially agrees with that found in other insects which have been investigated. A similar indication in *Periplaneta americana* was made by Nijenhuis and Dresden (1955).

Schmitt (1959) describes the cervicothoracic nervous system of *Dissosteira carolina* and presents several areas of nerve homology with respect to *Chauliodes*

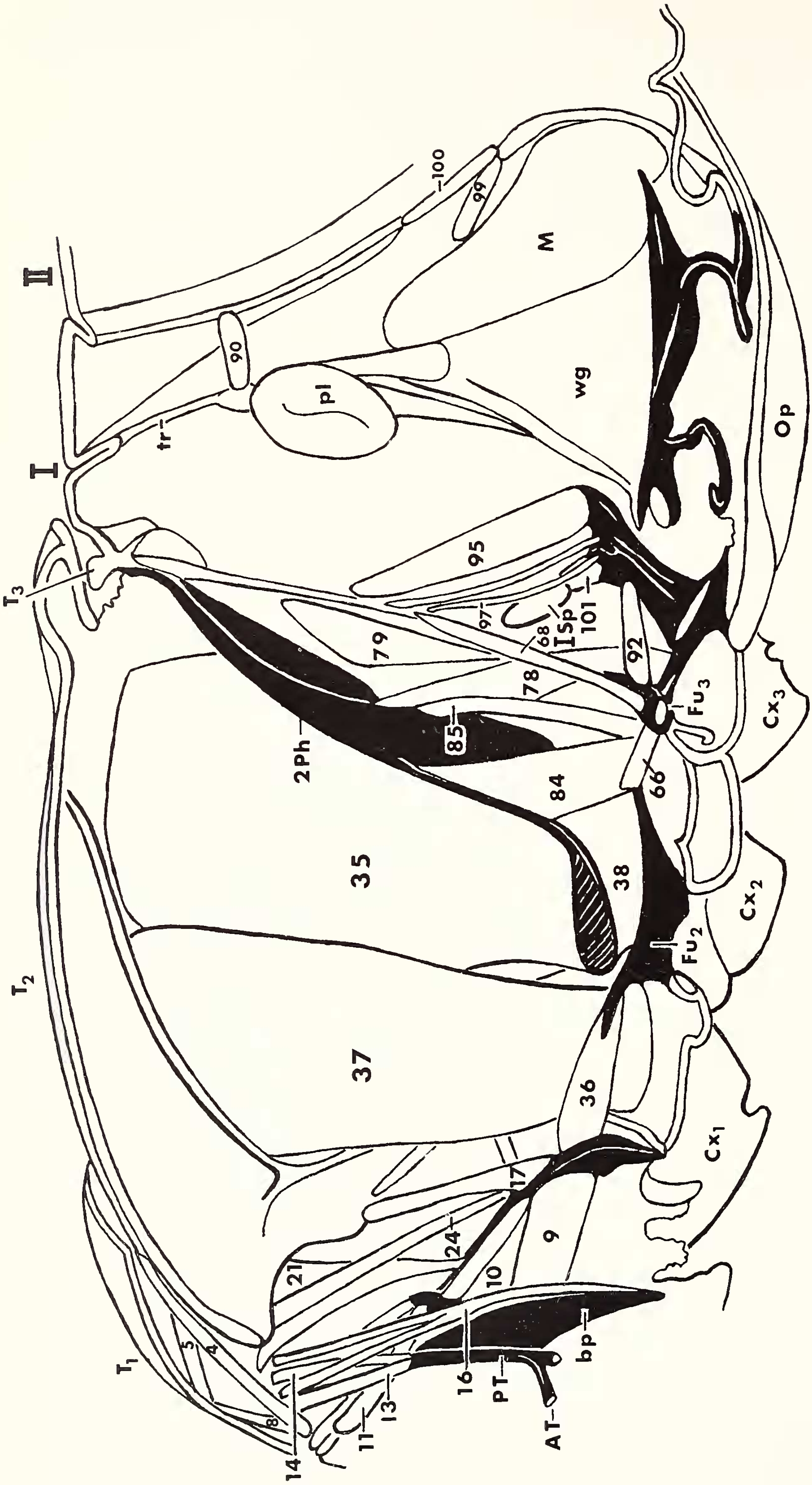

FIG. 3. Second stage dissection showing muscles of the cervix, thorax, and first abdominal segment in longitudinal section in the male annual cicada *Tibicen chloromera* (Walker).

formosanus as reported by Maki (1936). However, he states that the pterothoracic dorsal nerves pass beneath the ventral longitudinal muscles and differ in this respect from the prothoracic dorsal nerves of *Dissosteira* and all the thoracic dorsal nerves of *Chauliodes*. Schmitt compared the nerves of the prothoracic muscles of *Dissosteira* with those of the pterothorax and concluded that there is evidence of a loss of anterior prothoracic musculature as a result of the evolution of the cervix. The cephalic muscles of the cervical sclerites and the ventral lateral neck muscles are derived from this anterior prothoracic musculature. Schmitt also includes a comparative study of the anterior ganglionic connectives of the dorsal nerves of *Dissosteira*, *Periplaneta*, and *Orchelimum* and indicates that the anterior ganglionic connectives of the dorsal nerves may have a wider distribution than in Orthoptera but are not recognizable because of juxtaposition with the connectives of the ventral nerve cord. Schmitt describes the median nerves and the innervation of the spiracular muscles in *Dissosteira* and mentions that the transverse nerves, dorsal nerves, and the innervation of the spiracular muscles of *Chauliodes* as described by Maki (1936) present a pattern identical with that in *Dissosteira*. There appears to be no essential differences in the innervation pattern of the thoracic spiracles as compared with the innervation pattern of the abdominal spiracles in both *Chauliodes* and *Dissosteira*. Schmitt concludes that the nerves to the thoracic spiracles agree sufficiently with the nerve pattern of the abdominal spiracles to indicate that the thoracic spiracles may be homologous with the abdominal spiracles.

Schmitt (1962), in a later paper, despite unfortunate differences in nomenclature applied by different workers, presents additional information establishing the presence of nerve homologies in several insects. Schmitt utilizes the dorsal longitudinal muscles as a starting point since these muscles are homologous both in the thorax and abdomen of insects. Usually, from a descriptive standpoint it is quite simple to identify the dorsal nerves to these muscles. Schmitt arranges in tabular form the names and designations used by various authors for the nerves to the thoracic dorsal longitudinal muscles, designations of the anterior ganglionic connectives, designations of the subesophageal nerves to the protergal muscles, and a comparison of thoracic nerve designations used by various authors with those utilized by Maki for *Chauliodes*. The wing nerves, median and transverse nerves, innervation of the ventral muscles and spinosternal musculature, and a discussion of the prothoracic nervous system in various insects is also presented.

4. THE MUSCULATURE AND INNERVATION OF THE SOUND MECHANISM

The majority of investigations appearing in the literature concerning the sound mechanism of cicadas describes the construction of the sound apparatus and the mechanics of sound production. Myers (1928) presents a summary of the studies pertaining to the sound-producing apparatus as well as including his

Table 3. Mesothoracic musculature of *Tibicen chloromera* (Walker).

Muscle	Muscle number	Origin (or attachment)	Insertion (or attachment)
Dorsal muscles			
Median dorsal	34	Anterior median portion of tergum	Median area of second phragma
Lateral dorsal	35	Middle of dorsolateral portion of tergum	Lateral portion of second phragma
Ventral muscles			
Longitudinal ventral	36	Profurcal arm	Anterior mesofurcal arm
Tergo-Sternal muscles			
Anterior tergo-sternal	37	Anterior portion of dorsolateral region of tergum	Ventrolateral sternal region
Posterior tergo-sternal	38	Ventral portion of second phragma	Posterior mesofurcal arm
Tergo-Pleural muscles			
Tergo-pleural	39	Anterolateral margin of tergum	Anterior margin of episternum
Tergo-pleural	40	Lateral margin of tergum	Anterior margin of episternum
Tergo-pleural	41	Lateral margin of tergum	Mesothoracic pleural arm
Tergo-pleural	42	Lateral margin of tergum	Prothoracic pleural arm
Tergo-pleural	43	Lateral margin of tergum	Wing process
Tergo-pleural	44	Lateral margin of tergum	Base of mesothoracic pleural arm
Pleural-axillary	45	Episternum	Third axillary sclerite
Pleural-axillary	46	Episternum	Third axillary sclerite
Pleuro-subalar	47	Posterior margin of epimeron	Subalar sclerite
Sterno-Pleural muscles			
Sterno-basalar	48	Anterodorsal portion of episternum	Ventrolateral sternal region
Furco-entopleural	49	Furcal arm of mesothorax	Pleural arm of mesothorax
Coxal muscles			
Tergal promotor	50	Anterolateral region of tergum	Trochantin
Trochantino-basalar	51	Laterodorsal margin of episternum	Trochantin
Trochantino-basalar	52	Anterolateral margin of episternum	Trochantin
Sternal promotor	53	Base of mesofurcal arm	Anterior basal rim of coxa
Tergal remotor	54	Anterolateral region of tergum	Posterior basal rim of coxa
Tergal remotor	55	Posterior dorsolateral region of tergum	By a tendon to posterior basal rim of coxa
Coxo-subalar	56	Posterior basal rim of coxa	Subalar sclerite
Sternal remotor	57	Posterior mesofurcal arm	Posterior basal rim of coxa
Sternal remotor	58	Mesofurcal arm	Posterior basal rim of coxa
Sternal adductor	59	Mesofurca	Mesal basal edge of coxa
Coxo-basalar	60	Dorsal margin of episternum	Anterolateral basal rim of coxa
Trochanteral muscles			
Tergal depressor	61	Anterolateral portion of tergum	Depressor apodeme of trochanter
Trochantero-basalar	62	Dorsal margin of episternum	Depressor apodeme of trochanter
Sternal depressor	63	Mesofurcal arm	Depressor apodeme of trochanter
Muscles of the spiracle			
Occlusor	64	Subspicularum	Ventral portion of atrial chamber

own findings based on *Melampsalta sericea* and *Melampsalta muta,* two species of cicadas found in New Zealand.

Complete studies regarding the musculature of the first abdominal segment which contains the sound-producing apparatus have been described for *Cicada* (= *Tibicen*) *plebeia* by Berlese (1909) and for *Huechys sanguinea* var. *philaemata* by Maki (1938). Berlese utilizes both Roman and Arabic numerals for muscle identification in his figures while descriptions of muscle attachments are included in the text. Berlese (1909) shows the structure of the sound mechanism in his figures 879 to 882. Berlese considers the sclerotized V-shaped structure, yAd_2 in his figure 880, as the furca of the second abdominal sternite. However, Carlet (1876), Vogel (1923) and Myers (1928) who have given this structure the most attention, ascribe it to the first abdominal segment. Maki (1938) shows the musculature of the sound mechanism in his figure 24 and utilizes Arabic numerals for muscle numbers. Maki presents in tabular form the muscles of the first six abdominal segments with their muscle numbers. Descriptions of the muscle attachments are not included in the text.

A complete presentation of the innervation pattern of the first abdominal segment of cicadas has not appeared in the literature. However, the auditory or tymbal nerves which innervate the large tymbal muscles have been mentioned by various writers since Binet (1894). Swinton (1880) traced the auditory nerve from the thoracic ganglionic mass, presumably in the mesothorax, to the abdomen and around the tymbal muscle. The auditory nerve then forms a ganglion which enters a groove. According to Vogel (1923) the auditory nerve arises in the ventral nerve strands and rises, running parallel with the body wall, in a sclerotized groove and passes dorsally to the sense organ, where its fibers run into the base of each sense cell. Myers (1928), in poorly preserved material, found a distinct nerve emerging on each side of the last thoracic–ganglionic mass and running parallel to a sclerotized ridge leading up to the auditory capsule. Myers (1928) states that it is very improbable that the auditory nerve should arise from the abdominal strands, as Vogel (1923) states.

Investigations utilizing electric stimulation of the auditory or tymbal nerve and the sympathetic nerve have appeared in the literature. Pringle (1954) concluded that the frequency of tymbal movements resulting from the contractions of the tymbal muscle exceeds the rhythm of tymbal nerve stimulation. Pringle also reported that an isolated tymbal muscle does not give multiplied rhythmic reactions when stimulated but functions the same as a common skeletal muscle. Hagiwara and Watanabe (1956) found that at a certain intensity and frequency of nerve stimulation, repetitive potentials up to ten or more resulted from each stimulus in the tymbal muscle, tymbal nerve, and motor neuron. Voskresenskaya and Svidersky (1960) investigated the electrical activity of the tymbal muscle, the tymbal nerve, and the sympathetic nerve during and

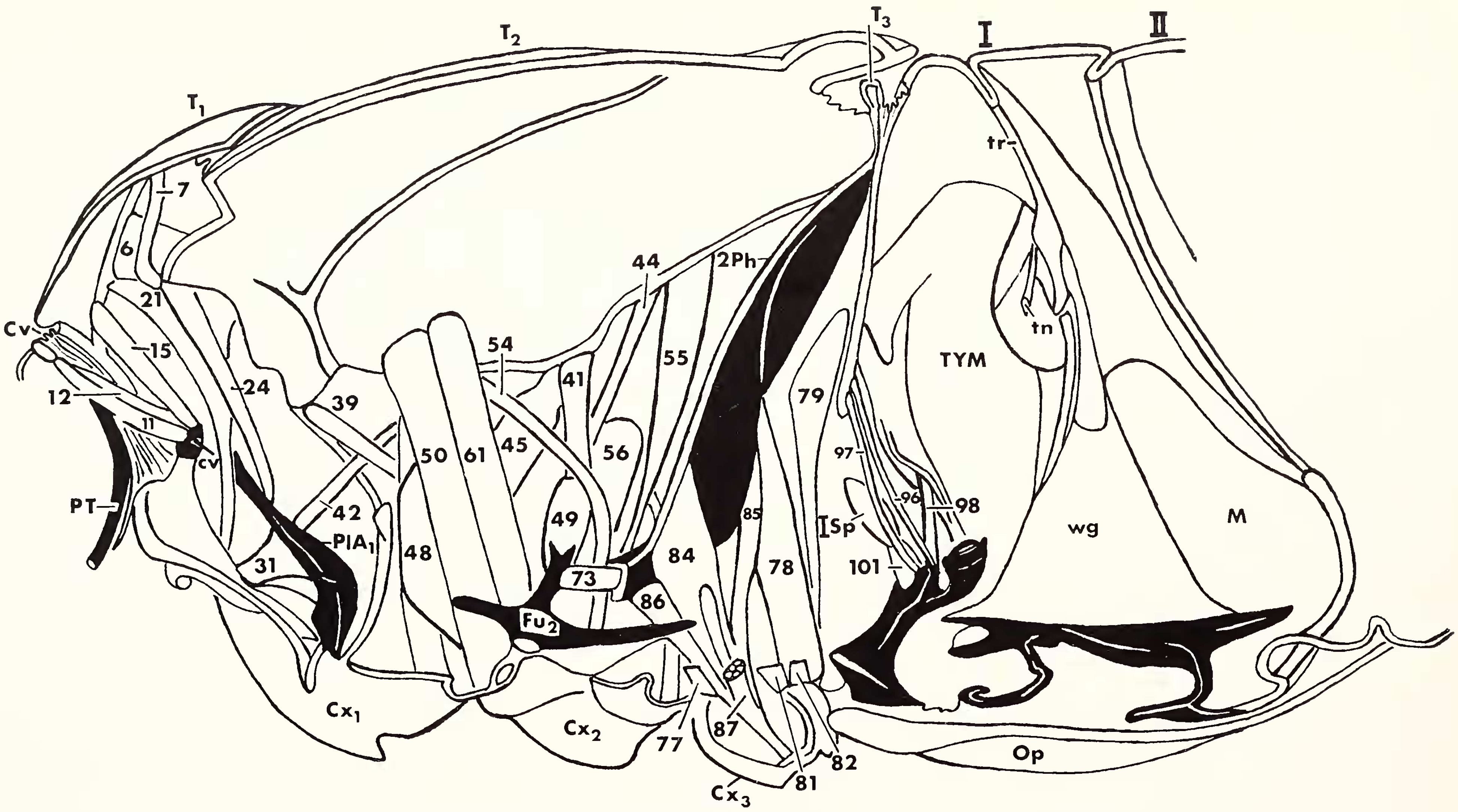

Fig. 4. Third stage dissection showing muscles of cervix, thorax, and first abdominal segment in longitudinal section in the male annual cicada *Tibicen chloromera* (Walker).

after electric stimulation and concluded that the sympathetic nervous system is essential to normal sound production in cicadas.

5. THE MUSCULATURE AND INNERVATION OF THE FOURTH ABDOMINAL SEGMENT

The musculature of the pregenital abdominal segments of male cicadas have been described by Maki (1938) for *Huechys sanguinea* var. *philaemata* and by Berlese (1909) for *Cicada* (= *Tibicen*) *plebeia*. Maki in his figure 24 shows the musculature of the first three abdominal segments and utilizes Arabic numerals for muscle numbers. Maki presents the muscles of the first six abdominal segments and their muscle numbers in a table on page 168 where he compares the musculature of *Erostus validus*, *Sigara substriata*, *Huechys sanguinea* var. *philaemata, Cicadella ferruginea,* and *Macrohomotoma gladiatum*. Maki does not describe the muscle attachments for *Huechys* in his text; however, they are clearly shown in his figure 24. Berlese (1909) describes the musculature of the first three abdominal segments in *Cicada* (= *Tibicen*) *plebeia* and utilizes both Roman and Arabic numerals for muscle identification. Descriptions of the muscle attachments are included in the text.

No studies dealing with the innervation of a pregenital abdominal segment of a male cicada have been found in the literature. Moreover, the literature contains only a few studies on the abdominal nervous system of insects.

In recent years some interest has been shown regarding the establishment of basic segmental nerve pattern within the Hexapoda. Schmitt (1954) describes the nervous system of the pregenital abdominal segments of *Dissosteira carolina*, *Acheta assimilis*, *Periplaneta americana*, and *Diapheromera femorata*. Schmitt utilizes various points of nerve homology or "landmarks" in presenting the innervation pattern of the above insects. The innervation of the ventral diaphragm in *Dissosteira* is also described. Libby (1959) describes the musculature and innervation of the second and third abdominal segments of the cecropia larva and concludes that the dorsal, ventral, and transverse nerve roots arising from each segmental ganglion of the cecropia larva seem homologous with those described by Schmitt (1954) for the pregenital segments of certain Orthoptera. Libby concludes, by utilizing the points of nerve homology set forth by Schmitt, that the homogeneity of the innervation pattern in such widely separated orders as Orthoptera and Lepidoptera lend further support to the concept of a basic segmental nerve pattern within the Hexapoda. Libby (1961) describes the musculature and innervation in the fourth abdominal segment of the adult male cecropia moth *Hyalophora cecropia* and compares his finding with the pregenital abdominal segments of *Chauliodes formosanus*, as described by Maki (1936), *Acheta assimilis*, as described by Schmitt (1954), and the larva of *Hyalophora*, as described by Libby (1959).

Schmitt (1963) describes the abdominal nervous system in the nymph of *Pteronarcys proteus* and the adult of *Pteronarcys californica* and concludes that

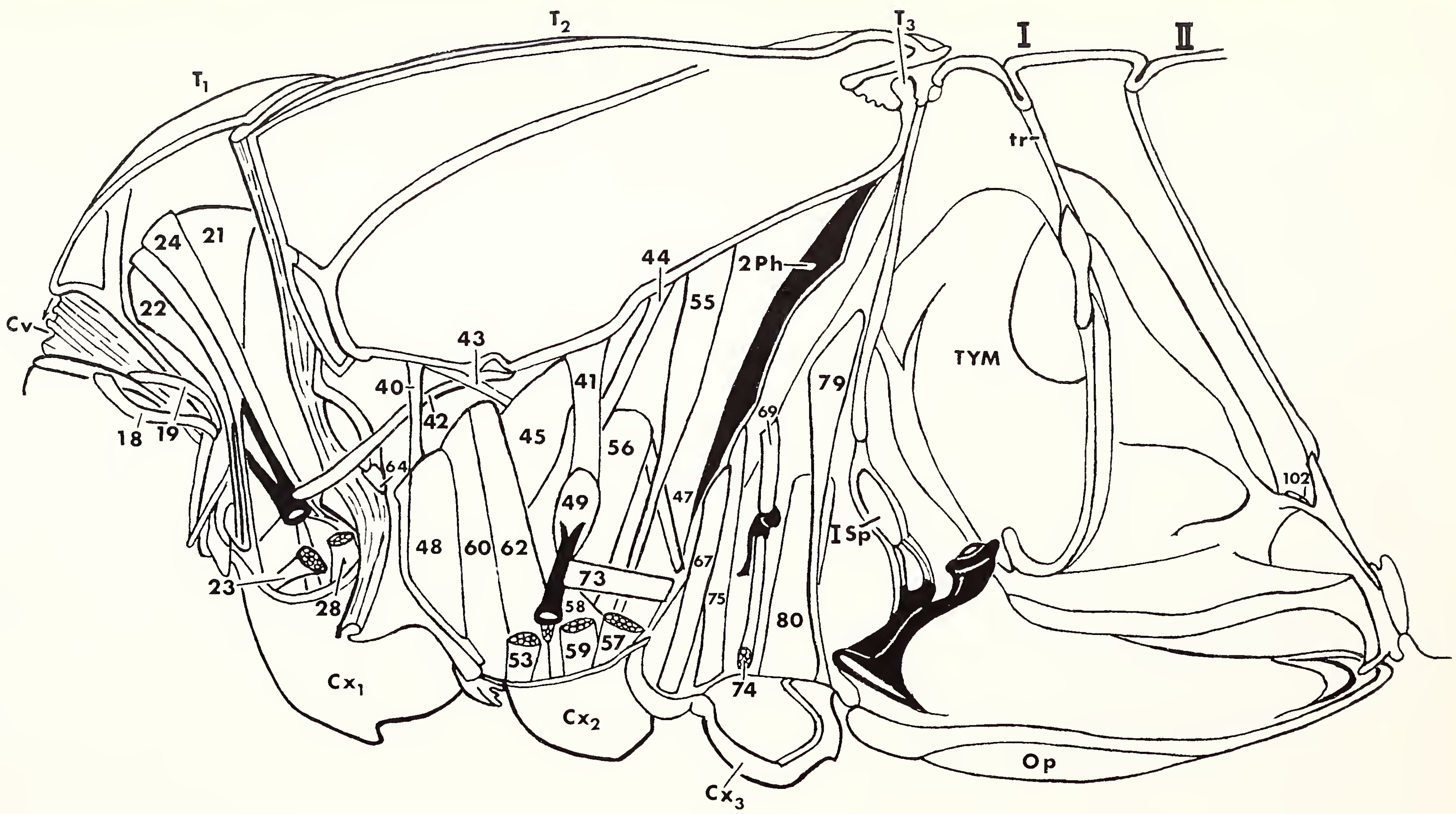

Fig. 5. Fourth stage dissection showing muscles of the cervix, thorax, and first abdominal segment in longitudinal section in the male annual cicada *Tibicen chloromera* (Walker).

the ganglia of segments 3 and 4 have coalesced and only the first three segments contain both dorsal and ventral nerves. The transverse nerves of segments 4, 5, and 6 arise from the ganglia of the immediately following segments. No occlusor or dilator muscles of the spiracles could be found in the two above-mentioned species of *Pteronarcys.* Schmitt also describes the muscles and nerves of the genital segments.

Schmitt (1964) describes the nerve pattern of the pregenital abdominal segments of *Neoconocephalis exiliscanorus* and *Ceutophilus gracilipes gracilipes,* two Orthoptera classified in the family Tettigoniidae. The segmental nerve patterns of these two insects were comparable and conformed to the patterns described in the Acrididae, the Gryllidae, and the Blattidae, as described by Schmitt (1954), and in *Carausius* (Phasmidae) as described by Marquardt (1939). Similarities in the nerve patterns to *Hyalophora cecropia* as described by Libby (1959 and 1961) and by Beckel (1958) and in some degree to the Plecoptera and the Megaloptera were noted. No innervation to the alary muscles could be found in *Neoconocephalus* or *Ceutophilus.*

Schmitt (1965) presents a comparative study on the transverse nerves of the pregenital abdominal segments of insects. By comparing the segmental innervation patterns of *Periplaneta, Neoconocephalus, Hyalophora, Chauliodes, Pteronarycs, Acroneurai, Apis,* and *Tibicen,* Schmitt concludes that, in those insects which apparently lack median and transverse nerves, these nerves are incorporated in the longitudinal connectives and lateral segmental nerves.

MATERIALS AND METHODS

Insect Material Used in the This Study.—The male of the annual cicada, *Tibicen chloromera* (Walker), was selected for this study in order to provide information concerning the musculature and nervous system of the thorax, sound mechanism, and a typical pregenital abdominal segment. The annual cicada's large size and ready availability make them especially attractive subjects for such investigation.

Nomenclature.—Nomenclature used in this study involve primarily the musculature and nervous system. Various methods of nomenclature have been devised for each of these organ systems.

Nomenclature of the musculature is based on the general outline set forth by Maki (1938) in his work on *Huechys sanguinea* var. *philaemata.* Muscles are named according to their position, attachment, or function and are assigned Arabic numerals which serve as muscle numbers in figures.

Effective nerve nomenclature requires not only that it describe the nerves in question, but also that it can be applied or adapted to as many nervous systems as possible in order to demonstrate nerve homologies. However, before a standard terminology can be devised, it is essential to have a relatively thorough knowledge of the musculature and nervous systems of many different insect

Table 4. Metathoracic Musculature of *Tibicen chloromera* (Walker)

Muscle	Muscle Number	Origin (or attachment)	Insertion (or attachment)
Dorsal muscles			
Median dorsal	65	Dorsal portion of second phragma	Dorsal portion of third phragma
Ventral muscles			
Longitudinal ventral	66	Posterior mesothoracic furcal arm	Metafurcal arm
Tergo-Sternal muscles			
Anterior tergo-sternal	67	Anterior dorsolateral region of tergum	Ventrolateral sternal region
Posterior tergo-sternal	68	Anterolateral edge of first abdominal tergum	Metafurcal arm
Tergo-Pleural muscles			
Tergo-pleural	69	Lateral portion of tergum	Pleural arm of metathorax
Tergo-pleural	70	Lateral portion of tergum	Dorsal border of episternum
Pleuro-axillary	71	Pleural ridge	Third axillary sclerite
Pleuro-axillary	72	Pleural ridge	Third axillary sclerite
Sterno-Pleural muscles			
Sterno-pleural	73	Mesofurcal arm	Anterior end of metathoracic episternum
Furco-entopleural	74	Metafurcal arm	Pleural arm of metathorax
Coxal muscles			
Tergal promotor	75	Anterior dorsolateral region of tergum	Trochantin
Pleural promotor	76	Anterior portion of episternum	Anterior basal rim of coxa
Sternal promotor	77	Metafurcal arm	Anterior basal rim of coxa
Tergal remotor	78	Mid dorsolateral region of tergum	Posterior basal rim of coxa
Tergal remotor	79	Posterior dorsolateral region of tergum	Posterior basal rim of coxa by a tendon
Coxo-subalar	80	Lateral basal rim of coxa	Subalare
Sternal remotor	81	Metafurcal arm	Posterior basal rim of coxa
Sternal remotor	82	Metafurcal arm	Posterior basal rim of coxa
Pleural abductor	83	Anterior region of episternum lateral to 75	Anterolateral basal rim of coxa
Trochanteral muscles			
Tergal depressor	84	Second phragma	Depressor apodeme of trochanter
Tergal depressor	85	Anterior portion of dorsolateral region of tergum	Depressor apodeme of trochanter
Pleural depressor	86	Episternum	Depressor apodeme of trochanter
Sternal depressor	87	Metafurcal arm	Depressor apodeme of trochanter
Muscles of the spiracle			
Occlusor	88	Ridge between mesothorax and metathorax	Ventral end of spiracle

species. Several systematic methods of nerve terminology have been devised and each have their advantages and disadvantages.

The method of nerve designation utilized in this paper is similar to that used by Whittig (1955) in her work on *Perla abdominalis* Burm. Ganglia, except for the subesophageal ganglion, are assigned Roman numerals. Nerve roots arising from each ganglion are designated by the Roman numeral of the ganglion followed by the letter N and an Arabic numeral. Lower case letters following Arabic numerals are used to identify nerve branches. Prime (′) and double prime (″) designations are utilized where it appears necessary for better understanding of nerve branch description.

Methods of Illustration.—Illustrations in this paper representing nerves and muscles are of two types. One type, the semiperspective illustration, is an attempt to represent as clearly as possible the various stages of dissection. Each stage is illustrated separately and in series beginning with the median muscle groups and progressing to the body wall. In illustrations that combine two consecutive stages of dissection, the lower half of the figure represents the earlier stage.

The second type of illustration used in this study are diagrams indicating the spatial relationships of nerves. The right side of the insect is illustrated and viewed in a laterad aspect. Muscle innervations are designated by Arabic numerals which represent muscle numbers. Where two nerves cross, the laterad nerve is interrupted. Nerves which terminate in the integument are indicated by a short line drawn across the nerve.

An explanation of abbreviated designations may be found under "Abbreviations used in the Figures" at the conclusion of this paper.

RESULTS AND DISCUSSION

1. THE VENTRAL NERVE CORD

General: The ventral nerve cord of insects is the postcephalic portion of the nervous system which lies beneath the alimentary canal and extends posteriorly through the thorax and abdomen. This portion of the central nervous system contains the subesophageal ganglion, thoracic ganglia, and abdominal ganglia arranged metamerically and joined by paired longitudinal connectives. However, modifications of the above generalized ventral nerve cord exists in a number of insect orders and is evidenced by the reduction in number or complete absence of ganglia in abdominal segments. Snodgrass (1935) states that there is a tendency for the ganglia of the ventral nerve cord to migrate anteriorly and unite with each other. This process is referred to as condensation. The forward migration and fusion of ganglia results in the shortening and external disappearance of connectives and commissures.

A dorsal view of the ventral nerve cord in the male cicada, *Tibicen chloromera* (Walker) is illustrated in Fig. 9 and consists of a subesophageal ganglion, prothoracic ganglion, and a thoracic–abdominal ganglionic mass. There are no ganglia in any of the abdominal segments. All abdominal segments are innervated by nerves originating from the posterior portion of the thoracic–abdominal ganglionic mass located in the mesothorax.

The subesophageal ganglion is the anterior ganglion of the ventral nerve cord.

TABLE 5. Comparison of prothoracic musculature of *Tibicen chloromera*, *Huechys sanguinea* var. *philaemata* (Maki, 1938), and *Cicada* (= *Tibicen*) *plebeia* (Berlese, 1909).

Muscle groups	*Tibicen chloromera*	*Huechys sanguinea* var. *philaemata* (Maki, 1938)	*Cicada* (= *Tibicen*) *plebeia* (Berlese, 1909)
Dorsal muscles			
Median dorsal	4	1	140
Median dorsal	5	2	CIX
Lateral dorsal	6	3	110
Lateral dorsal	7	–	CXII
Anterior dorsal	8	4	CXXXVI
Anterior dorsal	–	–	CXXXV
Ventral muscles			
Internal ventral	9	5	136
External ventral	10	6	CXXXI
Tergo-Sternal muscles			
Anterior intersegmental	11	7	147
Anterior internal tergo-sternal	12	–	–
Anterior internal tergo-sternal	13	8	CXXXV
Anterior internal tergo-sternal	14	–	–
Anterior internal tergo-sternal	15	9	CXXXVa
Anterior internal tergo-sternal	–	10	144
Anterior internal tergo-sternal	16	11	–
Posterior tergo-sternal	17	12	112
Tergo-Pleural muscles			
Anterior tergo-pleural	18	13	–
Anterior tergo-pleural	19	–	–
Ordinary tergo-pleural	20	14	–
Coxal muscles			
Tergal promotor	21	15	113
Tergal promotor	22	16	–
Sternal promotor	23	17	–
Tergal remotor	24	18	116
Tergal remotor	25	19	–
Tergal remotor	26	20	–
Tergal remotor	27	21	–
Sternal remotor	28	–	–
Tergal abductor	29	22	–
Pleural abductor	30	23	–
Pleural abductor	31	24	–
Trochanteral muscles			
Tergal depressor	32	25	115
Pleural depressor	33	26	–

In *Tibicen chloromera* eight pairs of nerves arise from the ganglion and innervate the salivary glands and lateral salivary gland ducts, muscles associated with the feeding apparatus, and some muscles of the cervical area.

The prothoracic ganglion and the anterior portion of the thoracic–abdominal ganglionic mass are covered dorsally by ventral muscles (Fig. 1B). Dufour (1833) mentions similar ventral muscles in *Cicada orni*.

An invagination of the first abdominal sternite serves as a muscle attachment for the large tympanal muscles. A sternal canal is located within this invagination. Two pairs of nerves, IIN8 and IIN9, pass through the sternal canal.

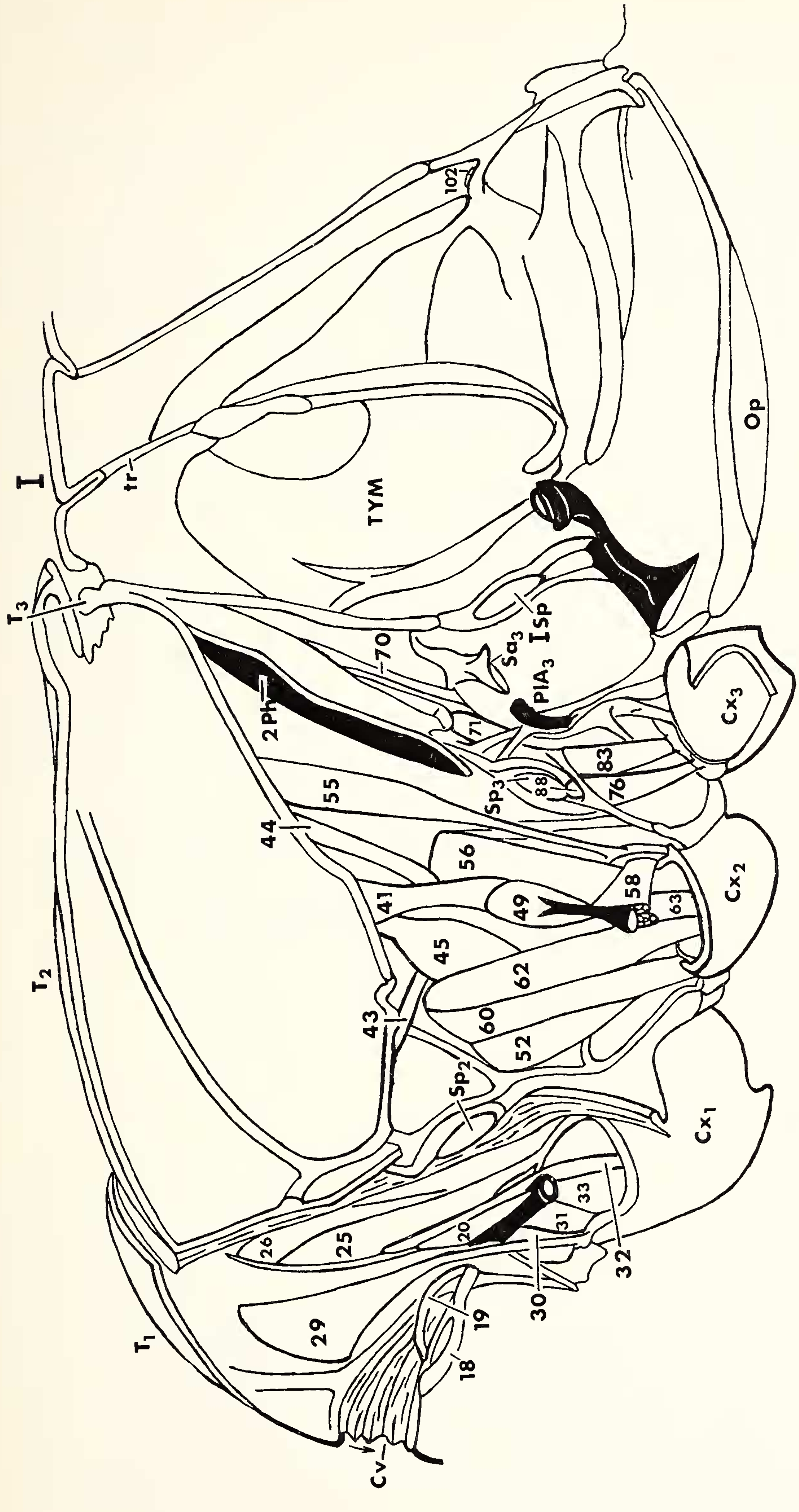

FIG. 6. Fifth stage dissection showing muscles of the cervix, thorax, and first abdominal segment in longitudinal section in the male annual cicada *Tibicen chloromera* (Walker).

One pair of nerves, IIN8, innervates the posterior muscles of the first abdominal segment while the other pair of nerves, IIN9, innervates the remaining abdominal segments.

No median nerve is visible between the subesophageal ganglion, prothoracic ganglion, and thoracic–abdominal ganglionic mass. However, the median nerve is probably included within the interganglionic connectives.

Spiracular muscles in the thoracic segments are innervated by nerves which arise from the dorsolateral portion of the prothoracic ganglion and thoracic–abdominal ganglionic mass. Spiracular muscles in pregenital abdominal segments are innervated by a nerve branch from the dorsal nerve.

The ventral nerve cord of the male *Tibicen chloromera* (Walker) is not restricted to a definitive positional relationship in the thorax by spinae or muscles that attach to these structures. Schmitt (1959) described an opposite situation in the thorax of *Dissosteira*, where possible future evolution of the ventral nerve cord towards condensation will require drastic skeletal and muscle system changes.

Subesophageal Ganglion: The anterior portion of the subesophageal ganglion is covered by the tentorial bridge (TB, Fig. 9). A pair of short, stout circumesophageal connectives link the subesophageal ganglion to the brain.

A lateral view of the subesophageal ganglion is shown in Fig. 1A. Eight pairs of nerves arise from the ganglion, five pairs of nerves from the lateroventral surface, and three pairs from the ventral area.

The first pair of nerves, SN1, arise from the anterior medioventral surface of the ganglion in close association with the ventral portions of the circumesophageal connectives. SN1 nerves divide into labral nerves (LmNv) and nerves which innervate the protractor muscles of the mandibular bristles (pmdb).

The second pair of nerves, SN2, are mandibular nerves and arise from the anterior lateroventral surface of the ganglion. The SN2 nerve divides soon after leaving the ganglion into a dorsal branch that innervates the retractor muscle of the mandibular bristle (rmdb) and a ventral branch that innervates the protractor muscles of the mandibular bristles.

The third pair of nerves, SN3, are maxillary nerves and arise from the lateroventral surface of the ganglion. The SN3 nerve bifurcates into anterior and posterior nerve branches. The anterior branches innervate the internal ($rmxb_1$) and the external ($rmxb_2$) retractor muscles of the maxillary bristles. Posterior nerve branches innervate both internal and external retractor muscles of the maxillary bristles, protractor muscles of the maxillary bristles (1pmxb and 2pmxb), and provide nerve branches which enter the base of the maxillary bristles, mxb (Fig. 1A).

The fourth, SN4, and fifth, SN5, pairs of nerves arise from the mediolateral and posterolateral areas, respectively, of the subesophageal ganglion and co-

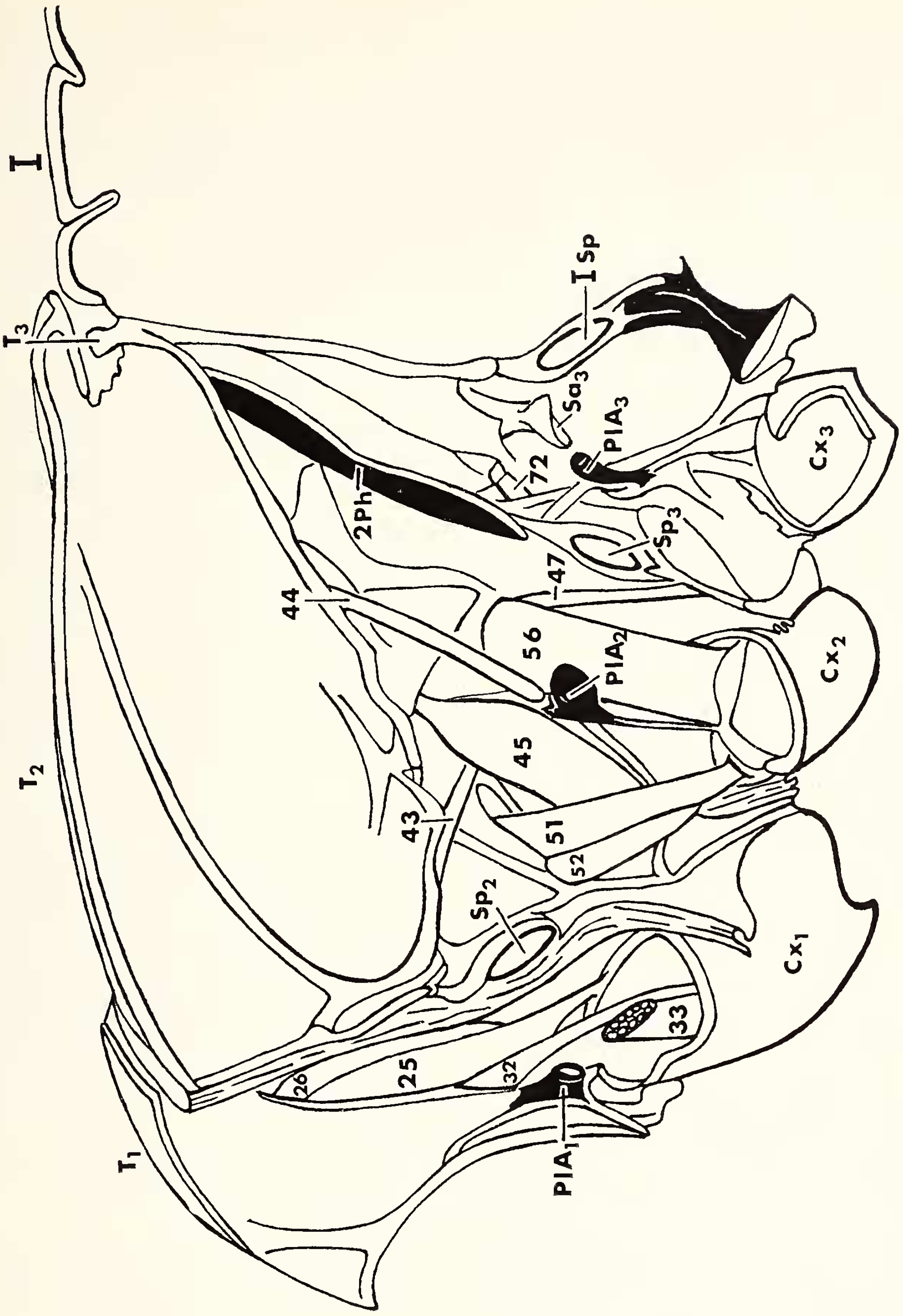

FIG. 7. Sixth stage dissection showing muscles of the thorax in longitudinal section in the male annual cicada *Tibicen chloromera* (Walker).

alesce to form the first cervical nerve SN4 + SN5. The SN4 + SN5 nerves extend dorsally and innervate the anterior internal tergo-sternal muscle 13.

The sixth pair of nerves, SN6, arises from the posterior lateroventral surface of the ganglion and innervates the salivary glands (S1G1) and the anterior internal tergo-sternal muscle 16. The latter nerves are the second cervical nerves. A nerve branch from SN6, and SN6a, proceeds in a posterior direction and coalesces with the SN9 + IN1 nerve.

The seventh pair of nerves, SN7, are the labial nerves and arise from the posterior medioventral surface of the ganglion ventrad to SN6. Nerve SN7 provides nerve branches to the dilator muscles of the salivary syringe (dlSyr) and the lateral muscles of the sclerotized rod (mr) before entering the labium. Johansson (1957) shows a similar innervation pattern for the labial nerve in the milkweed bug *Oncopeltus fasciatus* (Dallas). The labial nerves innervate the dilator muscles of the salivary syringe before entering the base of the labium.

The eighth pair of nerves, SN8, arises from the posterior medioventral surfaces of the ganglion in close association with the interganglionic connectives and innervates the salivary ducts (S1D).

A pair of large nerves, SN9, arises laterally from each interganglionic connective and coalesce with the IN1 nerves which arise from the anterior surface of the prothoracic ganglion. IN1 nerves can easily be separated from the interganglionic connectives to their origin on the prothoracic ganglion.

A pair of long, sturdy, well-separated interganglionic connectives link the subesophageal ganglion to the prothoracic ganglion. The interganglionic connectives pass laterally around the muscles of the sclerotized rod. The sclerotized rod is an extension of the labium and appears to have a stronger association with the prothorax than with the head since it hangs freely from the cervical membrane.

Prothoracic Ganglion: The prothoracic ganglion lies wholly within the prothorax and is situated between the sternal apophyses. Three pairs of ventral muscles (1, 2, and 3) cover the entire ganglion dorsally (Fig. 1B).

Four pairs of nerves arise from the anterior portion of the prothoracic ganglion (Fig. 9). The anterior pair of nerves (IN1) proceed anteriorly and join nerves SN9 which branch from the interganglionic connectives. Nerves IN2, IN3, and IN4 pass under the internal ventral longitudinal muscles (9) and innervate muscles of the cervix, prothorax, and prothoracic leg muscles. (A detailed description of the innervation pattern is presented under the section entitled "The Cervicothoracic Nervous System.")

A pair of large nerves, IIN1, issues from the interganglionic connectives between the prothoracic ganglion and thoracic–abdominal ganglionic mass (Fig. 9). The IIN1 nerves pass over the IIN2 nerves originating from the thoracic–abdominal ganglionic mass and then pass under the longitudinal ventral muscles 36 of the mesothorax. Nerve IIN1 innervates the longitudinal ventral muscles 36, median dorsal muscles 34, and lateral dorsal muscles 35 of the mesothorax.

A pair of fine, short nerves, IN5, arise on each side of the middorsal portion of the prothoracic ganglion and innervates the ventral muscles 1 which cover the ganglion.

Two pairs of fine nerves, IN6 and IN7, arise from the middorsal area of the prothoracic ganglion and coalesce with nerve IN8 arising from the dorsal surface of the interganglionic connective between the prothoracic ganglion and thoracic–abdominal ganglionic mass.

A pair of very short, stout interganglionic connectives links the prothoracic ganglion to the large thoracic–abdominal ganglionic mass.

Thoracic–Abdominal Ganglionic Mass: The thoracic–abdominal ganglionic mass is the terminal ganglion of the ventral nerve cord and is located above the basisternum of the mesothorax. With the exception of the IIN2a nerves which innervate the posterior tergo-sternal muscles 17 of the prothorax, nerves originating from the thoracic–abdominal ganglionic mass innervate muscles of the mesothorax, metathorax, sound mechanism, and abdominal segments.

Eight pairs of lateral nerve roots arise from the thoracic–abdominal ganglionic mass: one pair anteriorly, IIN2; two pairs laterally, IIN3 and IIN4; and five pairs posteriorly, IIN5, IIN6, IIN7, IIN8, and IIN9 (Fig. 9). Nerves IIN2, IIN3, and IIN4 pass under the longitudinal ventral muscles 36 while the remaining nerve roots extend posteriorly and pass over the mesofurca. IIN2 is the anterior wing nerve while IIN3 and IIN4 innervate muscles in the mesothorax. Nerves IIN5 and IIN6 pass under the posterior arms of the mesofurca and innervate muscles of the metathoracic segment with the exception of nerve branch IIN6a′ which innervates the posterior tergo-pleural muscle 38 of the mesothorax. The IIN5 nerve is the dorsal nerve since it innervates the dorsal muscles 65. Ventral muscles are innervated by a nerve branch from IIN10 + IIN11. Nerve IIN6 provides a nerve branch IIN6a which is the posterior wing nerve. Nerves IIN7 supply innervation to the muscles located in the anterior portion of the first abdominal segment and the membrane forming the large abdominal air chamber. Nerves IIN8 provide nerve branches IIN8a to the large tympanal muscles before passing through the sternal canal to innervate the muscles located in the posterior portion of the first abdominal segment. The IIN9 nerves pass through the sternal canal and innervate muscles of the remaining pregenital abdominal segments by providing a lateral nerve branch to each consecutive segment. Two pairs of fine nerves (IIN10 and IIN11) arise dorsolaterally from the thoracic–abdominal ganglionic mass (Fig. 9). The IIN11 nerve divides soon after leaving the ganglion and provides a fine nerve branch IIN11a which coalesces with nerve IIN5. Nerves IIN10 and IIN11 are connected by a fine nerve designated as IIN10 + IIN11. It appears that both the IIN10 and IIN11 nerves are responsible for innervation of the occlusor muscle (88) of the metathoracic spiracle and ventral muscle 3.

Discussion: Unfortunately, only the gross anatomy of the central nervous system of cicadas has been described in the literature. Therefore, comparisons of ventral nerve cords in order to establish areas of homology are limited to their general configuration.

Hilton (1939) in his Figure 190–1 presents an unlabeled drawing of the central nervous system of an unnamed adult cicada showing the brain and two ganglia of the ventral nerve cord. If it is assumed that the anterior ganglion is the

TABLE 6. Comparison of mesothoracic musculature of *Tibicen chloromera*, *Huechys sanguinea* var. *philaemata* (Maki, 1938), and *Cicada* (= *Tibicen*) *plebeia* (Berlese, 1909).

Muscle groups	*Tibicen chloromera*	*Huechys sanguinea* var. *philaemata* (Maki, 1938)	*Cicada* (= *Tibicen*) *plebeia* (Berlese, 1909)
Dorsal muscles			
Median dorsal	34	27	70
Median dorsal	–	–	69
Lateral dorsal	35	28	71
Ventral muscles			
Longitudinal ventral	36	29	105 + 106
Spino-furcal ventrals	–	–	104
Tergo-Sternal muscles			
Anterior tergo-sternal	37	30	LXXVIII
Posterior tergo-sternal	38	31	73
Tergo-Pleural muscles			
Tergo-pleural	39	32	XCI
Tergo-pleural	40	33	86
Tergo-pleural	41	34	–
Tergo-pleural	42	–	–
Tergo-pleural	43	–	–
Tergo-pleural	44	–	–
Pleuro-axillary	45	35	XCIII
Pleuro-axillary	46	36	XCII
Pleuro-subalar	47	37	–
Sterno-Pleural muscles			
Sterno-basalar	48	38	91
Furco-entopleural	49	39	100
Coxal muscles			
Tergal promotor	50	40	74?
Trochantino-basalar	51	–	79 + 80
Trochantino-basalar	52	–	–
Sternal promotor	53	41	–
Tergal remotor	54	42	LXXXII
Tergal remotor	55	43	75
Coxo-subalar	56	44	84
Sternal remotor	57	45	–
Sternal remotor	58	–	–
Sternal adductor	59	–	–
Pleural abductor	–	46	–
Coxo-basalar	60	47	82
Trochanteral muscles			
Tergal depressor	61	48	76
Trochantero-basalar	62	49	81
Sternal depressor	63	50	–
Muscles of the spiracle			
Occlusor	64	51	–

subesophageal ganglion, then the remaining ganglionic mass contains all of the thoracic and abdominal ganglia.

Dufour (1833), describing the ventral nerve cord in *Cicada orni*, states that the central nervous system consists of a cephalic ganglion and two thoracic ganglia. No mention is made of the subesophageal ganglion, which, according to Myers (1928), Dufour may have confused with the brain. Dufour does mention that the cephalic ganglion is produced by a fusion of two hemispheroid lobes and the cleft which separates the two lobes is only superficial. Dufour continues by describing the thoracic ganglia as not being separate and distinct but nearly fused into one. However, with difficulty, a light demarcation of an anterior ganglion can be observed.

Myers (1928) states that the ventral nerve cord in *Melampsalta sericea* consists of a subesophageal ganglion, prothoracic ganglion, and thoracic–abdominal ganglionic mass, each separated by visible interganglionic connectives.

Berlese (1909), in his Figure 697, presents a diagram of the brain and the subesophageal ganglion of *Cicada* (= *Tibicen*) *plebeia*, and shows that the subesophageal ganglion is separated from the brain by a pair of stout circumesophageal connectives. The remainder of the ventral nerve cord is not described.

Snodgrass (1935), in his Figure 237, presents a longitudinal section of *Tibicina* (= *Magicicada*) *septendecim* showing two thoracic ganglia, one in the prothorax and the other in the mesothorax. The subesophageal ganglion is not illustrated.

If the above investigations are correct, then there appears to be some diversity in the family Cicadidae regarding the number of ganglia in the ventral nerve cord. *Cicada orni* is the most specialized with a central nervous system composed of a cephalic ganglion and two very closely associated thoracic ganglia while in *Melampsalta sericea* and *Tibicen chloromera* there is a subesophageal ganglion and two separate thoracic ganglia.

There also appears to be a diversity in the number of principal lateral nerve roots arising from the thoracic ganglia. Dufour (1833) mentions that the anterior thoracic ganglion in *Cicada orni* gives rise to four pairs of principal nerves while six pairs of nerves issue from the posterior thoracic ganglion. Hilton (1939), in his Figure 190–1, of the central nervous systems of an unnamed species of cicada, shows three principal nerves arising from the anterior lobe of the thoracic–abdominal ganglionic mass while the posterior lobe possesses three pairs of lateral nerves and a single caudal nerve.

Tibicen chloromera has three pairs of principal lateral nerve roots (not counting the IN1 nerve which adheres to the interganglionic connective) arising from the prothoracic ganglion. One nerve, IIN1, appears to arise from the interganglionic connective between the prothoracic ganglion and thoracic–abdominal ganglionic mass, and eight principal pairs of nerves arise from the thoracic–abdominal ganglionic mass.

2. THORACIC MUSCULATURE

General: The thoracic musculature of the male cicada, *Tibicen chloromera* (Walker) is illustrated in Figs. 1B to 8. Figs. 2 to 8 represent stage dissections which proceed from the interior muscle groups to the exterior muscle groups on the body wall. Arabic numerals are utilized for muscle numbers. Thoracic

Table 7. Comparison of metathoracic musculature of *Tibicen chloromera, Huechys sanguinea* var. *philaemata* (Maki, 1938), and *Cicada* (= *Tibicen*) *plebeia* (Berlese, 1909).

Muscle groups	*Tibicen chloromera*	*Huechys sanguinea* var. *philaemata* (Maki, 1938)	*Cicada* (= *Tibicen*) *plebeia* (Berlese, 1909)
Dorsal muscles			
Median dorsal	65	52	37
Ventral muscles			
Longitudinal ventral	66	53	68
Tergo-Sternal muscles			
Anterior tergo-sternal	67	54	XXXVI
Posterior tergo-sternal	68	55	XXXVII
Tergo-Pleural muscles			
Tergo-pleural	69	56	–
Tergo-pleural	70	–	–
Pleuro-axillary	71	57	56
Pleuro-axillary	72	58	–
Sterno-Pleural muscles			
Sterno-pleural	73	59	–
Furco-entopleural	74	60	65
Coxal muscles			
Tergal promotor	75	61	42?
Pleural promotor	76	62	48 + 49
Sternal promotor	77	63	–
Tergal remotor	78	64	44
Tergal remotor	79	65	43
Coxo-subalar	80	66	XLIX
Sternal remotor	81	67	61
Sternal remotor	82	–	–
Pleural abductor	83	68	–
Trochanteral muscles			
Tergal depressor	84	69	XLV
Tergal depressor	85	70	46
Pleural depressor	86	71	–
Sternal depressor	87	72	–
Muscles of the spiracle			
Occlusor	88	73	–

muscles are listed with their muscle numbers, origins, and insertions in Tables 1 to 4. A comparison of the thoracic musculature of *Tibicen chloromera, Huechys sanguinea* var. *philaemata* described by Maki (1938) and *Cicada* (= *Tibicen*) *plebeia* described by Berlese (1909) is presented in Tables 5 to 7.

Ventral Muscles Which Cover the Thoracic Ganglia: The prothoracic ganglion and the anterior portion of the thoracic–abdominal ganglionic mass are covered dorsally by three pairs of muscles (Fig. 1B). The muscle numbers, origins, and insertions of the three muscles groups are described in Table 1. Ventral muscles 1, 2, and 3 are mutually joined by zygomatic connections. Muscles 1 and 3 are quite sturdy, while muscle 2 is broad at its zygomatic junction and compressed dorsoventrally. Muscle 3 is joined laterally to ventral longitudinal muscle 36 for a portion of its length.

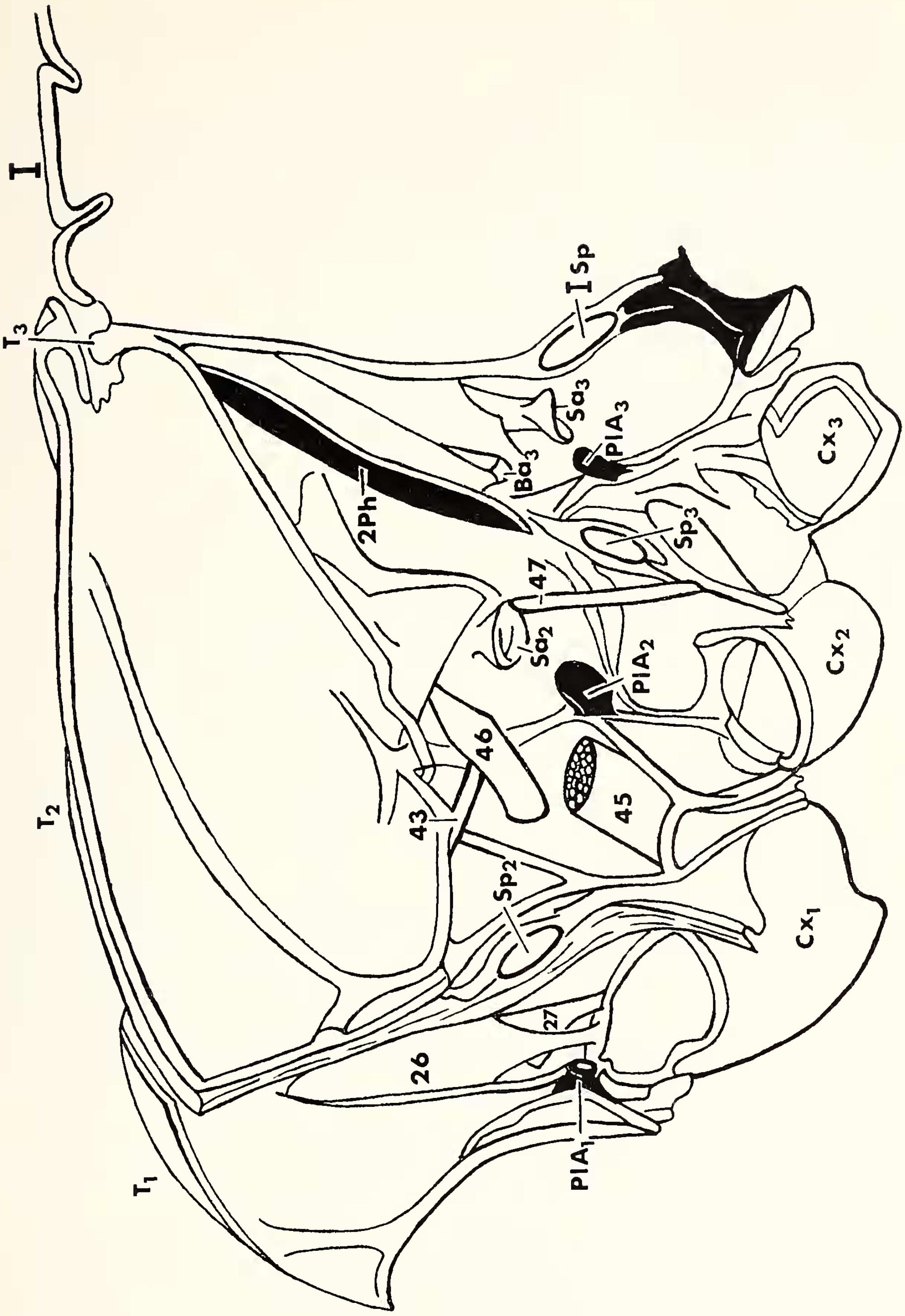

Fig. 8. Seventh stage dissection showing muscles of the thorax in longitudinal section in the male annual cicada *Tibicen chloromera* (Walker).

Prothoracic Musculature: The prothoracic muscles in *Tibicen chloromera* are fundamentally homologous to *Huechys sanguinea* var. *philaemata* (Table 5). The lateral dorsal 7, anterior internal tergo-sternals 12 and 14, anterior tergo-pleural 19, and sternal remotor 28 muscles in *Tibicen chloromera* were not reported in *Huechys sanguinea* var. *philaemata.*

The anterior internal tergo-sternal muscle 10 reported by Maki (1938) and muscle 144 by Berlese (1909) are absent in *Tibicen chloromera.* This muscle arises on the tergum and attaches to the ventrolateral cervical sclerite. However, the anterior tergo-sternal muscles 12 in *Tibicen chloromera*, which has its origin on the posterior end of the head and attaches to the ventrolateral cervical sclerite, is probably the homologue.

Berlese (1909) did not report the presence of tergo-pleural, sternal promotor, sternal remotor, tergal abductor, pleural abductor or pleural depressor muscles in the prothorax of *Cicada* (= *Tibicen*) *plebeia*. The anterior internal tergosternal 14, anterior tergo-pleural 19, and sternal remotor 28 muscles in *Tibicen chloromera* do not have counterparts in the other two species of cicadas.

Mesothoracic Musculature: The mesothorax is the largest division of the thorax and necessarily so, since it contains the very large dorsal longitudinal (34) and oblique dorsal (35) muscles. The dorsal longitudinal muscles serve as depressors of the wings while the oblique dorsal muscles are probably wing elevators (Snodgrass, 1927 and 1935).

The tergo-pleurals 42, 43, and 44, trochantino-basalar 52, sternal remotor 58, and sternal adductor 59 muscles in *Tibicen chloromera* have not been reported in *Huechys sanguinea* var. *philaemata* by Maki (1938) or in *Cicada* (= *Tibicen*) *plebeia* by Berlese (1909). The trochantino-basalar muscle 51 in *Tibicen chloromera* is present in *Cicada* (= *Tibicen*) *plebeia* (79 + 80) but not in *Huechys sanguinea* var. *philaemata*. The pleural abductor of the coxa, Maki's muscle number 46 in *Huechys sanguinea* var. *philaemata*, was not described by Berlese (1909) in *Cicada* (= *Tibicen*) *plebeia* nor is it present in *Tibicen chloromera*.

Berlese (1909) includes median dorsal 69 and spino-furcal ventral 104 muscles in *Cicada* (= *Tibicen*) *plebeia*. Both of the above muscles are not present in the two other species of cicadas (Table 6). Berlese (1909) did not report the presence of pleural-subalar, sternal promotor, sternal remotor, sternal adductor, sternal depressor, or spiracular muscles.

Metathoracic Musculature: The metathorax is extremely short, especially dorsally, where the entire notum is reduced to a narrow band behind the scutellum of the mesonotum.

The metathoracic musculature in *Tibicen chloromera* is homologous to that of *Huechys sanguinea* var. *philaemata*, with the exception of the tergo-pleural muscle 70 and the sternal remotor muscle 82. Berlese (1909) did not report the presence of tergo-pleural, sternal-pleural, sternal promotor, pleural abductor, pleural depressor, sternal depressor, and spiracular muscles. However, all of the above mentioned muscles were reported by Maki (1938) in *Huechys sanguinea* var. *philaemata* and are present in *Tibicen chloromera*.

3. THE CERVICOTHORACIC NERVOUS SYSTEM

General: A dorsal view of the ventral nerve cord in the male of *Tibicen chloromera* (Walker) is shown in Fig. 9. A general description of the thoracic nervous system is presented under the section entitled "The Ventral Nerve Cord."

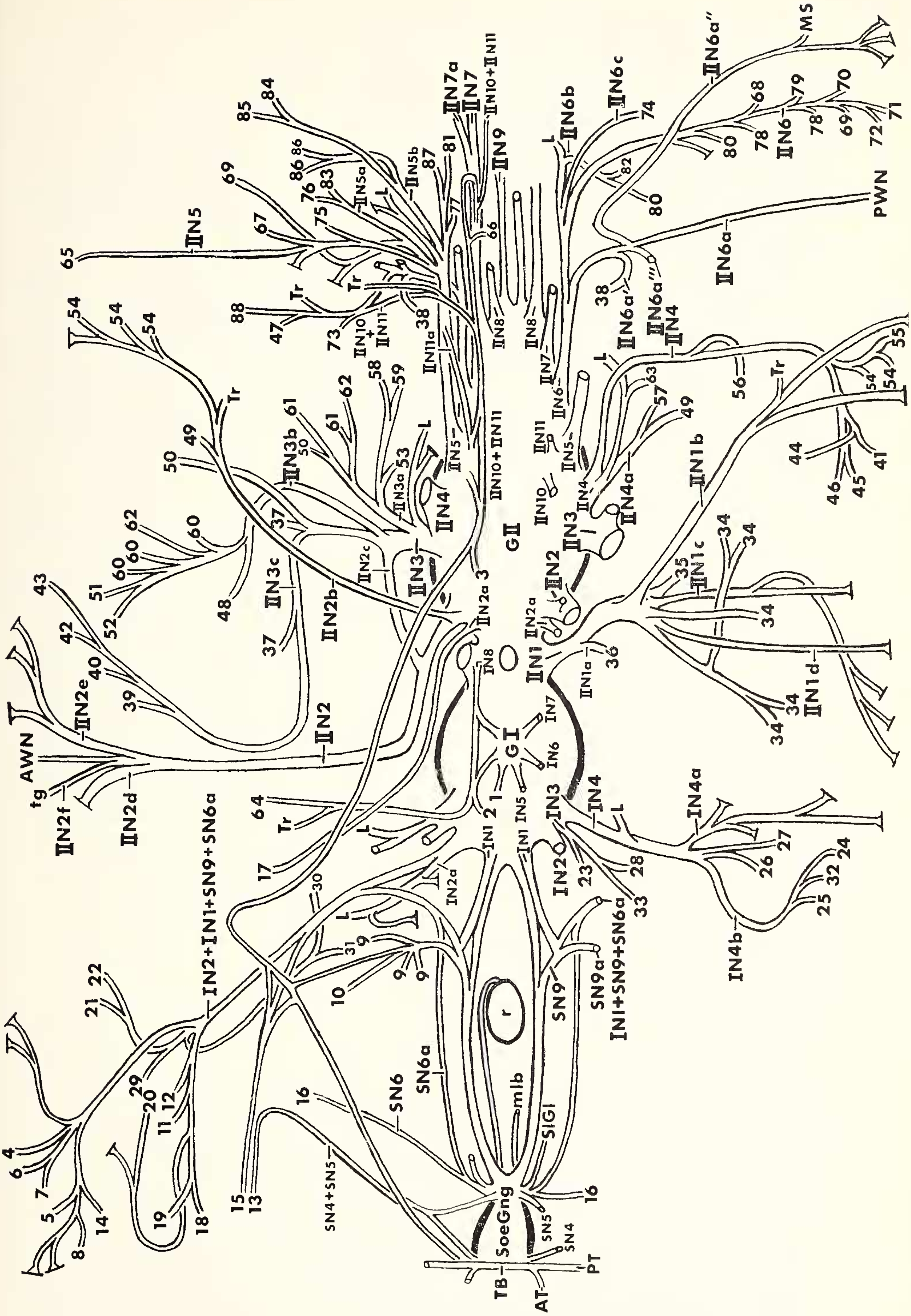

FIG. 9. Dorsal view of the ventral nerve cord of the male annual cicada *Tibicen chloromera* (Walker) from the head to the first abdominal segment.

The Cervix and the Prothorax: The narrowed membranous region between the head and prothorax of insects is called the cervix or neck and is presumably derived from portions of both the labial and prothoracic segments. Muscles contained within the cervical region are believed to have evolved from both the labial and prothoracic segments. Therefore, the concept that the muscles of a segment are innervated from the ganglion of that segment suggests that each muscle of the cervix can be assigned either to the labial or prothoracic segment by determining the segment of innervation.

Three pairs of nerves from the subesophageal ganglion innervate muscles located in the cervical region: SN4 + SN5, SN6 (Fig. 9), and SN7 (Fig. 1A). Nerve SN4 + SN5 innervates the anterior intersegmental muscle 13 and nerve SN6 innervates the anterior intersegmental muscle 16. The SN7 nerve innervates the muscles of the sclerotized rod, mr, and muscles within the labium, mlb (Fig. 1A). The sclerotized rod is an extension of the labium and hangs freely from the cervical membrane.

A nerve branch from SN6, designated as SN6a in figs. 1A and 9, may be associated with the innervation of the anterior intersegmental muscle 15 and possibly other muscles in the cervicoprothoracic area. A precise determination could not be made since the SN6a nerve joins with a nerve formed by the coalescence of nerves SN9 and IN1. The resulting nerve, IN1 + SN9 + SN6a, then coalesces with the IN2 nerve to form nerve IN2 + IN1 +SN9 +SN6a which innervates muscles associated with the cervical sclerites, dorsal muscles, and muscles located in the anterior portion of the prothorax.

The SN9 nerves issue from the interganglionic connectives between the subesophageal ganglion and prothoracic ganglion. Nerve branch SN9a innervates the internal ventral muscle 9 and external ventral muscle 10 before joining the IIN10 + IIN11 nerve originating from the thoracic–abdominal ganglionic mass (Fig. 9). Nerve SN9 then coalesces with nerve IN1 and later receives the SN6a nerve before joining nerve IN2 originating from the prothoracic ganglion.

The IN1 nerves arise from the anterior portions of the prothoracic ganglion adjacent to the interganglionic connectives. Nerves IN1 proceed anteriorly in close association with the interganglionic connectives before coalescing with the SN9 nerves.

The IN2 nerves issue from the anterolateral area of the prothoracic ganglion and pass under the internal ventral muscles 9. The first nerve branch, IIN2a, provides two sensory nerve branches to the integument, then passes around the tergal promotor muscle of the coxa 21 and over the anterior basal rim of the prothoracic coxa into the leg. After IN2 coalesces with nerve IN1 + SN9 + SN6a to produce nerve IN2 + IN1 + SN9 + SN6a, a nerve branch is formed which combines with nerve branches from nerve IIN10 + IIN11 to innervate the anterior intersegmental muscle 15. Nerve IN2 + IN1 + SN9 + SN6a then

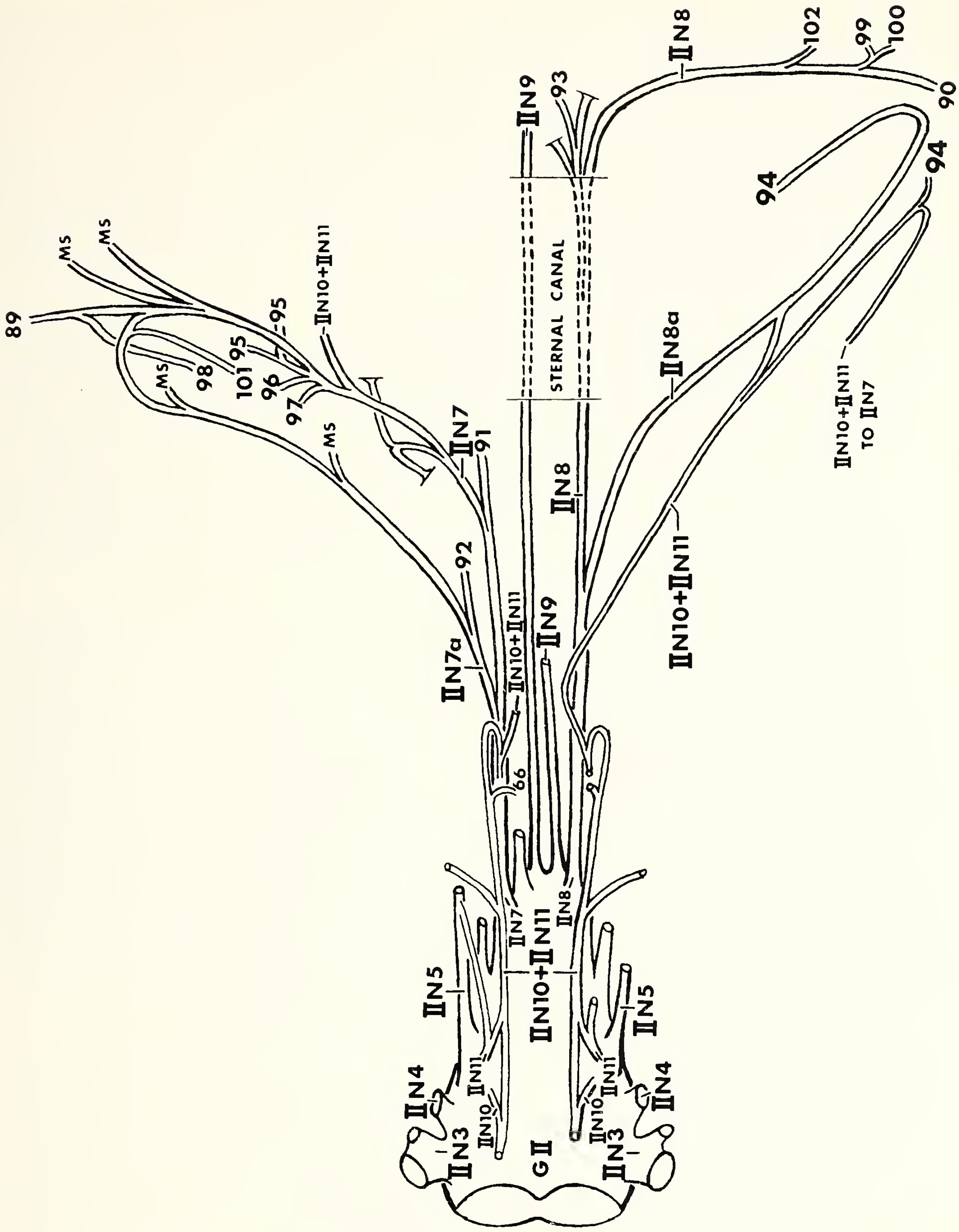

Fig. 10. Dorsal view of the ventral nerve cord of the male annual cicada, *Tibicen chloromera* (Walker), from nerve root IIN3 of the thoracic–abdominal ganglionic mass to the second abdominal segment and showing the innervation pattern of the first abdominal segment.

ramifies into three nerve branches. One nerve branch proceeds anteriorly and innervates the anterior intersegmental muscles 11 and 12, the ordinary tergo-pleural muscle 20, and the anterior tergo-pleural muscles 18 and 19. The lateral nerve branch bifurcates into a ventral branch which innervates the pleural abductors 30 and 31 and a dorsal branch which innervates the tergal abductor muscle 29 and the tergal promotor muscles 21 and 22. The remaining nerve branch proceeds dorsally and innervates the anterior intersegmental muscle 14, anterior dorsal muscle 8, median dorsal muscle 5, lateral dorsal muscles 6 and 7, and median dorsal muscle 4.

The IN3 nerves arise from the anterolateral portion of the prothoracic ganglion, pass under the anterior edge of the prothoracic pleural apophysis, and innervate the sternal promotor 23, pleural depressor 33, and sternal remotor 28 muscles.

Nerve IN4 arises from the anterolateral portion of the prothoracic ganglion posterior to IN3 and proceeds in a lateral direction passing under the prothoracic pleural apophysis. IN4 provides a nerve branch into the leg before dividing into nerve branches IN4a and IN4b. IN4a is a sensory nerve and provides nerve branches to the posterolateral protergal area. Nerve IN4a innervates tergal remotor muscles 24, 25, 26, and 27 and the tergal depressor muscle 32.

Nerve IN5 is very short and issues from the mediodorsal area of the prothoracic ganglion and innervates ventral muscle 1.

Nerves IN6 and IN7 arise from the mediodorsal portion of the ganglion posterior to nerve IN5 and coalesce with nerve IN8 which arises from the dorsal area of the interganglionic connective between the prothoracic ganglion and thoracic–abdominal ganglionic mass (Fig. 9). It appears that nerves IN6, IN7, and IN8 are responsible for the innervation of ventral muscle 2 and the occlusor muscle 64 of the mesothorax.

The posterior tergo-sternal muscle 17 of the prothorax is innervated by nerve branch IIN2a which arises from the anterolateral area of the thoracic–abdominal ganglionic mass. Nerve IIN2a passes under nerve IIN1 and proceeds lateral to the longitudinal ventral muscle 36 and along the posterior edge of the prothoracic pleural arm to the posterior tergo-sternal muscle 17.

Mesothorax: The mesothorax is the largest thoracic segment in the male of the annual cicada, *Tibicen chloromera* (Walker). Innervation of the mesothoracic segment, with the exception of the posterior tergo-sternal muscle 38 and the occlusor muscle 64, is achieved by five pairs of nerves: IIN1, IIN2, IIN3, IIN4, and IIN10 + IIN11.

The large IIN1 nerves arise from the short interganglionic connectives between the prothoracic ganglion and thoracic–abdominal ganglionic mass GII (Fig. 9). Nerve IIN1 passes over nerve IIN2 and provides nerve branch IIN1a to the longitudinal ventral muscle 36.

Nerve IIN1a bifurcates into two nerve branches. One nerve branch enters muscle 36 along its mesal surface while the remaining nerve branch enters the lateral surface of the muscle 36. The IIN2 nerve passes laterad to the longitudinal ventral muscle 36 and ramifies into six nerve branches along the ventral edge of the median dorsal muscle 34. The large median dorsal muscle 34 is innervated by three nerve branches while the lateral dorsal muscle 35 is in-

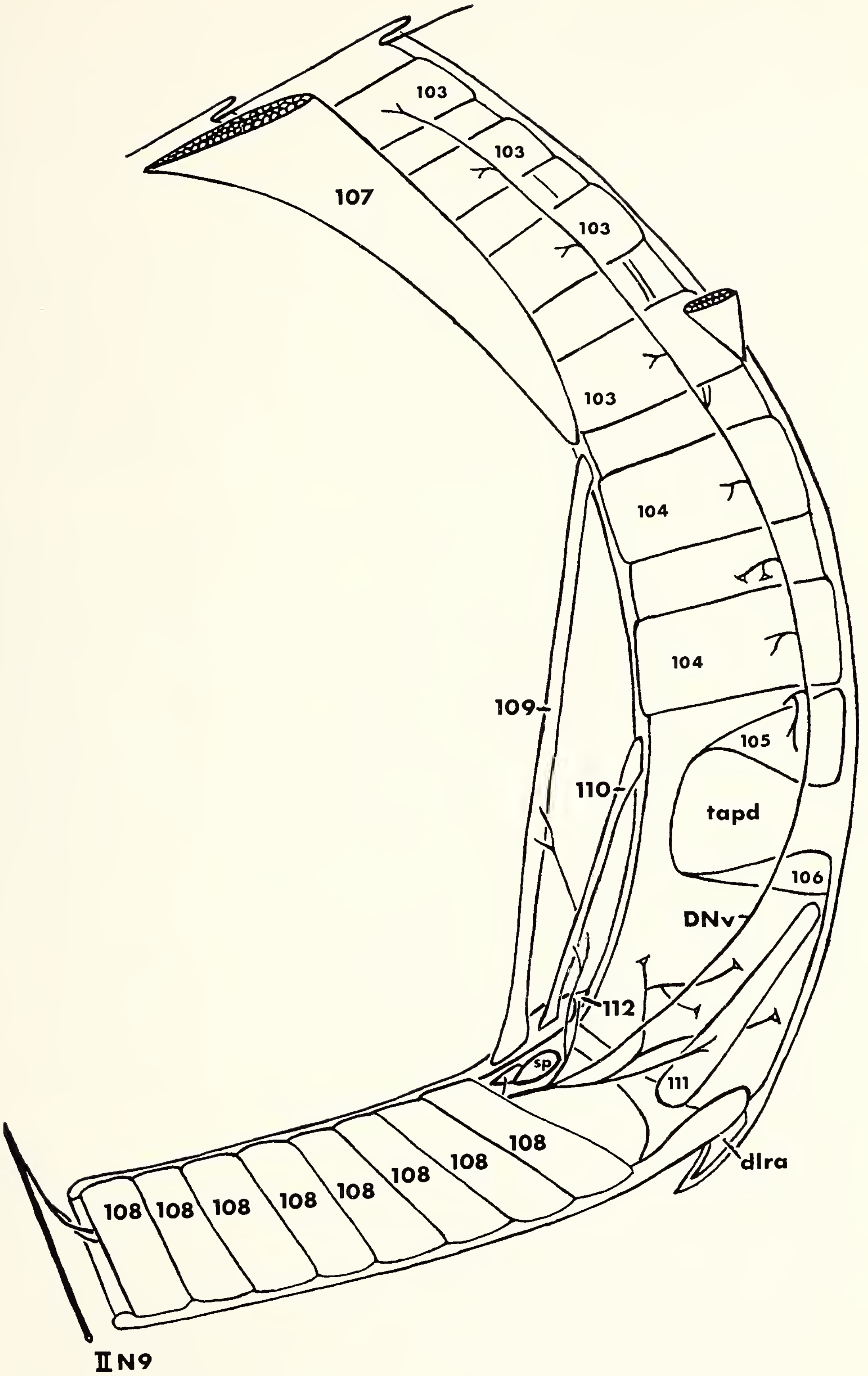

Fig. 11. Posterolateral view of the nerves and muscles of the right side of the fourth abdominal segment of the male of *Tibicen chloromera* (Walker). First stage of dissection.

nervated by a single nerve branch which passes between the median dorsal muscle 35 and the anterior tergo-sternal muscle 37. The remaining nerve branches (IIN1b, IIN1c, and IIN1d) are sensory nerves and terminate in the integument of the mesotergum (Fig. 9). Nerve branch IIN1b passes obliquely between the anterior tergo-sternal muscle 37 and the median dorsal muscle 34 and continues mesad to the furco-entopleural muscle 49 and tergal remotor muscle 54. Nerve IIN1b provides a nerve branch to the trachea between muscle 54 and 55 before terminating in the integument in the posterior portion of the mesotergum. IIN1c passes mesad to median dorsal muscle 34 and divides into two nerve branches. One nerve branch continues dorsally and terminates in the middorsal region of the mesotergum while the other nerve branch passes between the latter nerve and muscle 34 and terminates in the integument in the anterodorsal region of the mesotergum. Nerve IIN1d passes obliquely over the anterior tergo-sternal muscle 37 then proceeds along the posterior edge of muscle 37 and terminates in the integument of the middorsal region of the mesotergum.

Nerve IIN2 arises from the anterolateral surface of the thoracic–abdominal ganglionic mass. Two nerve branches, IIN2a and IIN2b, issue from the base of nerve IIN2. The IIN2 nerve passes under the ventral longitudinal muscle 36, and provides a nerve branch IIN2c to nerve IIN3 (Fig. 9). Nerve IIN2 proceeds anterodorsally along the posterior edge of the profurcal arm and then passes laterad to the anterior tergo-sternal muscle 37. The IIN2 nerve divides into three nerve branches, IIN2d, IIN2e, and IIN2f, prior to entering the forewing. Nerve branch IIN2d enters the integument below the tegula of the mesothorax. Nerve branch IIN2e terminates in the integument in the region of the third axillary sclerites and nerve branch IIN2f enters the mesothoracic tegula. Nerve IIN2 is the anterior wing nerve (AWN, Fig. 9) and enters the base of the mesothoracic wing. Nerve branch IIN2a innervates the posterior tergo-sternal muscle 17 of the prothorax. Nerve branch IIN2b passes under the ventral longitudinal muscle 36, proceeds around the posterior edge of the anterior tergo-sternal muscle 37, and innervates the furco-entopleural muscle 49 and the tergal remotor muscle 54, before terminating in the integument along the lateral edge of the mesotergum.

Nerve IIN3 is a large nerve and arises from the lateral surface of the thoracic–abdominal ganglionic mass. The first nerve branch passes under the nerve IIN4 and bifurcates into two nerve branches. One nerve branch enters the integument while the remaining nerve branch passes over the anterior basal aim of the mesothoracic coxa and enters the leg. Nerve branch IIN3a innervates the sternal promotor of the coxa 53, sternal remotor of the coxa 58, sternal adductor of the coxa 59, tergal depressor 61, trochantero-basalar 62, and the tergal promotor of the coxa 50. Nerve IIN3 is then connected to IIN2 by way of nerve branch IIN2c. The next nerve branch, IIN3b, innervates the sterno-basalar muscle 48, the trochantero-basalar muscle 62, the trochantino-basalar muscles 51 and 52, and the coxo-basalar muscle 60.

Nerve IIN3 then ramifies into three nerve branches, one innervating the anterior tergo-sternal muscle 37, another which innervates the tergal promotor muscle 50, and a nerve branch designated as IIN3c (Fig. 9). Nerve branch IIN3c innervates the anterior tergo-sternal muscle 37 and the tergo-pleural muscles 39, 40, 42, and 43.

Nerve IIN4 issues from the lateral surface of the thoracic–abdominal ganglionic mass posterior to IIN3 and proceeds posteriorly and ramifies into three nerve branches (Fig. 9). One nerve branch innervates the sternal depressor muscle of the coxa 63 before passing over the posterior basal rim of the coxa and into the mesothoracic leg. Nerve branch IIN4a innervates the furco-ento-pleural muscle 49 and the sternal remotor muscle 57. Nerve IIN4 passes around the posterior edge of the sternal remotor muscle 57 and provides a nerve branch to the coxo-subalar muscle 56. Nerve IIN4 continues dorsally and innervates the tergo-pleural muscles 41 and 44, the pleuro-axillary muscles 45 and 46, and the tergal remotor muscles 54 and 55.

The posterior tergo-sternal muscle 38 of the mesothorax is innervated by nerve branch IIN6a′. Nerve branch IIN6a is the posterior wing nerve (PWN, Fig. 9). It is noteworthy that the posterior tergo-sternal muscle 17 of the prothorax is innervated by a nerve branch IIN2a of the anterior wing nerve IIN2.

The pleuro-subalar muscle 47 is innervated by a nerve branch formed by the coalescence of IIN10 + IIN11 and nerve branch IIN6a‴.

Ventral muscle 3 is innervated by a nerve branch from the IIN10 + IIN11 nerve (Fig. 9).

Metathorax: The metathorax is the shortest thoracic segment in the male of the annual cicada, *Tibicen chloromera* (Walker). The entire notum is reduced to a narrow band behind the scutellum of the mesonotum (Fig. 2). Innervation of the metathoracic segment is achieved by three pairs of nerves: IIN5, IIN6, and IIN10 + IIN11 (Fig. 9).

Nerve IIN5 arises from the lateroposterior surface of the thoracic–abdominal ganglionic mass and passes mesad to the mesofurca. After receiving nerve branch IIN11a, nerve IIN5 continues posteriorly and ramifies into five nerve branches (Fig. 9). The anterior nerve branch, IIN5, is the dorsal nerve and innervates the tergal promotor muscle 75, the anterior tergo-sternal muscle 67, and terminates in the median dorsal muscles 65. The next nerve branch originates at the base of IIN5 and bifurcates into a nerve branch which enters the integument and nerve branch IIN5a which innervates the pleural promotor muscle 76 and the pleural abductor muscle 83. A nerve branch originating between IIN5 and IIN5b provides a nerve to the integument before passing over the anterior basal rim of the metathoracic coxa and into the leg. Nerve

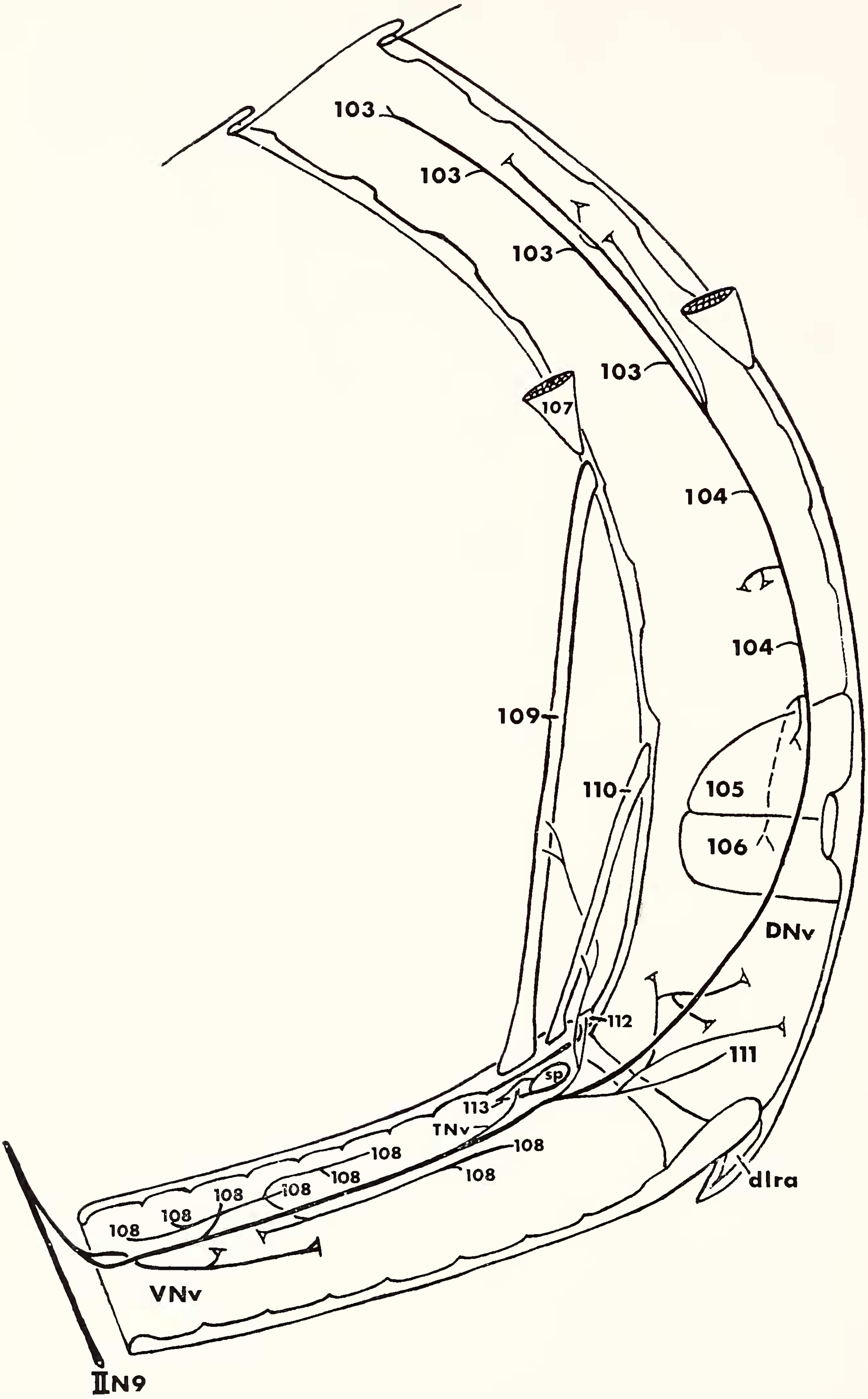

Fig. 12. Posterolateral view of the nerves and muscles of the right side of the fourth abdominal segment of the male of *Tibicen chloromera* (Walker). Second stage of dissection.

branch IIN5b passes under the posterior mesofurcal arm and provides a nerve branch to the pleural depressor muscle 86 before innervating the tergal depressor muscles 84 and 85. The remaining nerve branch innervates the sternal promotor muscle 77, the sternal depressor muscle 87, and the sternal remotor muscle 81.

Nerve IIN6 passes under the posterior mesofurcal arm and forms nerve branch IIN6a which passes around the posterior tergo-sternal muscle 38 of the mesothorax providing the nerve branch, IIN6a′ to muscle 38. Nerve branch IIN6a″ passes around the tergal depressor muscle 84 and proceeds along the posterior edge of the second phragma (2 Ph) and provides a nerve branch to the membranous sac of the abdominal air chamber (MS) before terminating in the integument along the posterolateral edge of the metatergum (Fig. 9). Nerve branch IIN6a‴ coalesces with nerve IIN10 + IIN11. Nerve IIN6a is the posterior wing nerve and passes along the anterior edge of the second phragma and enters the base of the metathoracic wing. Nerve IIN6 passes under the posterior metafurcal arm and proceeds dorsally along the posterior edge of the tergal remotor muscle 79. Nerve IIN6 provides a nerve branch which enters the integument of the epimeron before innervating the following muscles: coxo-subalar 80, posterior tergo-sternal 68, tergal remotors 78 and 79, tergo-pleural 69 and 70, and the pleural-axillary muscles 71 and 72. Nerve IIN6b provides a nerve branch to the metathoracic leg before innervating the sternal remotor muscles 82 and the coxo-subalar muscle 80. Nerve branch IIN6c innervates the furco-entopleural muscle 74.

Nerves IIN10 and IIN11 arise from the posterior dorsolateral surface of the thoracic abdominal ganglionic mass and coalesce to form nerve IIN10 + IIN11. The anterior branch of nerve IIN10 + IIN11 passes mesad to the ventral muscle 3 and provides a nerve branch to muscle 3 prior to passing mesad to the profurcal arm and the posterior tergo-sternal muscle 17 of the prothorax. Nerve IIN10 + IIN11 continues anteriorly passing over the large trachea of the mesothoracic spiracle and provides two nerve branches which coalesce with a nerve branch from IN2 + IN1 + SN9 + SN6a that innervates the anterior internal tergo-sternal muscle 15 of the prothorax. A nerve branch from SN9a also joins nerve IIN10 + IIN11. The pattern of axon distribution resulting from this fusion requires histological clarification. However, it appears that the anterior intersegmental muscle 15, which attaches to the anterior dorsolateral region of the protergum and the ventrolateral cervical sclerite, does, in part, receive its innervation from nerve IIN10 + IIN11. The IIN10 + IIN11 nerve continues anteriorly and passes under the tentorial bridge.

Nerve IIN11 provides a short nerve branch, IIN11a, that coalesces with nerve IIN5.

The posterior branch of IIN10 + IIN11 passes dorsally over the caudal portion of the thoracic–abdominal ganglionic mass and bifurcates into a dorsal branch and ventral branch. The dorsal branch divides forming two nerve branches. One nerve branch passes mesad to IIN6a′ and enters the large trachea originating from the metathoracic spiracle. The second nerve branch passes laterad to IIN6a′ and coalesces with IIN6a‴ to innervate the sterno-pleural muscle 73, the pleuro-subalar muscle 47 of the mesothorax, and the occlusor muscle 88 of the metathoracic spiracle. The ventral branch, IIN10 + IIN11, continues posteriorly and innervates the longitudinal ventral muscle 66, then forms a loop which proceeds anteriorly and provides a nerve branch which coalesces with nerve IIN7. The IIN10 + IIN11 nerve proceeds in a posterior direction and enters the first abdominal segment which contains the sound mechanism. Further description of the innervation pattern of the IIN10 + IIN11 nerve is presented under the section entitled "The Musculature and Innervation of the Sound Mechanism."

Nerve IIN7 innervates the muscles located in the anterior portion of the first abdominal segment while nerve IIN8 innervates the muscles located in the posterior portion of the first abdominal segment. The IIN9 nerves innervate the remaining pregenital abdominal segments by providing a pair of lateral nerve roots to each consecutive segment.

Discussion: The thoracic nervous system in the male of the annual cicada, *Tibicen chloromera* (Walker), presents a perplexing enigma regarding the determination of nerve homologies. This problem is due to the coalescence of the mesothoracic, metathoracic, and abdominal ganglia into a single ganglionic mass located in the mesothorax. Condensation of the ventral nerve cord has presumably resulted in the coalescence of lateral nerve branches thereby producing apparent variations in the nerve distribution pattern in *Tibicen* when compared to nerve patterns described in other insects.

Schmitt (1962) suggests utilization of the dorsal longitudinal muscles as a starting point in establishing nerve homologies. The dorsal longitudinal muscles are innervated by the dorsal nerves of each consecutive segment. Therefore, from a descriptive standpoint, it is usually easy to identify the dorsal nerve as it issues from its ganglion. However, Nüesch (1954) has shown that some of the axons which supply the dorsal longitudinal muscles also originate from the immediately anterior ganglion.

The dorsal muscles of the prothorax in *Tibicen* is innervated by nerve IN2 + IN1 + SN9 + SN6a. Nerve SN9 may be the anterior ganglionic connective of the dorsal nerve and has adhered to the interganglionic connective. However, it cannot be determined without recourse to histological examination if nerve IN1 or nerve IN2 is the prothoracic dorsal nerve.

The dorsal longitudinal muscles of the mesothorax are innervated by the IIN1 nerves which arise from the very short interganglionic connectives between the prothoracic ganglion and the thoracic–abdominal ganglion mass. Anterior ganglionic connectives are not visible in *Tibicen*. Nüesch (1954) has demonstrated in *Telea* that motor axons from the prothoracic ganglion pass through the anterior ganglionic connectives to the mesothoracic dorsal nerve. Anterior ganglionic connectives are not visible in *Chauliodes*, as described by Maki (1936), nor in *Agulla*, as described by Matsuda (1956). However, Schmitt (1962) proposes that if the findings of Nüesch regarding the innervation of the dorsal longitudinal muscles are applicable to other Neopterygota, it is probable that the fibers of the anterior ganglionic connectives are also present in *Chauliodes* and *Agulla*, but are incorporated in the interganglionic connectives to their connection with the dorsal nerves.

Nerve IIN5 in *Tibicen* is the dorsal nerve of the metathorax and provides innervation to muscles located in the anterior portion of this segment and the dorsal longitudinal muscles.

In the Neopterygota, wing nerves may also be useful in establishing nerve homologies. The wing nerve enters the wing cavity and is associated with sensory structures at the base of the wing. In *Tibicen* there are two wing nerves. The anterior wing nerve IIN2 arises from the anterolateral surface of the thoracic–abdominal ganglionic mass. Two nerve branches arise from the base of the anterior wing nerve (IIN2a and IIN2b) and a third nerve branch IIN2c coalesces with nerve IIN3 (Fig. 9). Nerve IIN2 then continues as a completely independent nerve providing sensory nerve branches to the integument below the tegula, the tegula, and the integument in the region of the third axillary sclerites before entering the wing cavity. Maki (1936) describes a similar condition in *Chauliodes*, where a separate nerve which he labeled "fourth root" arises from the mesothoracic ganglion and passes directly into the wing. In *Dissosteira*, Schmitt (1959) found that in addition to innervating the dorsal muscles of the mesothorax, the dorsal nerve also provides an anterior nerve branch which enters the tegmen anteriorly and a posterior branch, entering the same wing posteriorly. In *Agulla*, Matsuda (1956) also found that a branch of the dorsal nerve enters the wing. It appears that the wing nerves of *Tibicen* and *Chauliodes* are homologous to the wing nerves of *Dissosteira* and *Agulla* despite their association with dorsal nerves in the latter two insects. The posterior wing nerve in *Tibicen* arises as a nerve branch, IIN6a, from nerve IIN6 (Fig. 9). Nerve IIN6a provides three nerve branches, IIN6a′, IIN6a″, IIN6a‴, before continuing as a separate nerve and passing directly into the metathoracic wing cavity.

It is interesting to note that the thoracic legs receive their innervation from two pairs of nerves, one entering the coxae anteriorly and the other posteriorly. The prothoracic legs are innervated by nerve branches from nerves IN2 and IN4 and the mesothoracic legs by nerve branches from IIN3 and IIN4 while nerve branches from IIN5 and IIN6 enter the metathoracic legs.

In *Tibicen* no median nerves are visible between the subesophageal ganglion and the prothoracic ganglion nor between the prothoracic ganglion and the thoracic–abdominal ganglionic mass. However, the median nerves may be included within the interganglionic connectives. The transverse or lateral nerves to the occlusor muscles of the mesothoracic spiracles arise from the dorsal surface of the prothoracic ganglion. The mesothoracic occlusor muscle 64 is innervated by a nerve resulting from the coalescence of nerves IN6, IN7, and IN8 (Fig. 9). Case (1957) has shown that in the cockroach the axons to muscles of a thoracic spiracle leave the anterior ganglion by way of the median nerve, passing to the transverse nerve and then to the muscles. Hoyle (1959) has reported a similar axon path in the thorax of *Schistocerca gregaria.* It appears then that the nerve formed by the coalescence of IN6, IN7, and IN8 is in part the transverse nerve since it terminates in the occlusor muscle of the mesothoracic spiracle. In many instances the transverse nerves from the prothoracic ganglion coalesce with the mesothoracic dorsal nerves. This was found to be true in *Agulla* and *Blattella* by Matsuda, in *Carausiaus* by Marquardt (1939), in *Chauliodes* by Maki (1936), in *Dissosteira* by Schmitt (1959), in *Periplaneta* by Pipa and Cook (1959), in *Perla* by Wittig (1955), and in *Telea* by Nüesch (1957). Schmitt (1962) mentions that no explanation has been offered for the coalescence of dorsal nerves to the transverse nerves and presumably the transverse nerves provide other functions in addition to exercising control over the spiracles.

The IIN10 + IIN11 nerves may contain axons of a transverse nerve, since a nerve branch from IIN10 + IIN11 coalesces with nerve branch IIN6a‴ and the resulting nerve terminates in the occlusor muscle 88 of the metathoracic spiracle.

4. THE MUSCULATURE AND INNERVATION OF THE SOUND MECHANISM

General: The musculature of the sound mechanism of *Tibicen chloromera* (Walker) is shown in Figs. 2 to 4 and a list of these muscles with their muscle numbers and attachments is presented in Table 8. Fig. 10 shows that the innervation of the first abdominal segment is achieved by nerves IIN7, IIN8, and IIN10 + IIN11. Nerve branch IIN8a is the auditory or tymbal nerve since it innervates the large tergo-sternal muscle 94 or tymbal muscle of the sound mechanism. Nerve IIN10 + IIN11 provides nerve branches to IIN8a and the tymbal muscle.

The Musculature of the Sound Mechanism: The musculature of the sound mechanism of *Tibicen chloromera* (Walker) is contained within the first abdominal segment. The tergo-sternal muscle 94 (Fig. 2), or tymbal muscle, is the largest muscle of the sound mechanism and has its attachments on the basal portion of the first abdominal sternum and a sclerotized terminal plate which attaches to the tymbal by a tendon. The tymbal muscles and the tymbals are the essential elements of the sound-producing apparatus (Myers, 1928).

The first abdominal sternite has become modified into a sclerotized V-shaped structure which provides attachments and support for the large tymbal muscles.

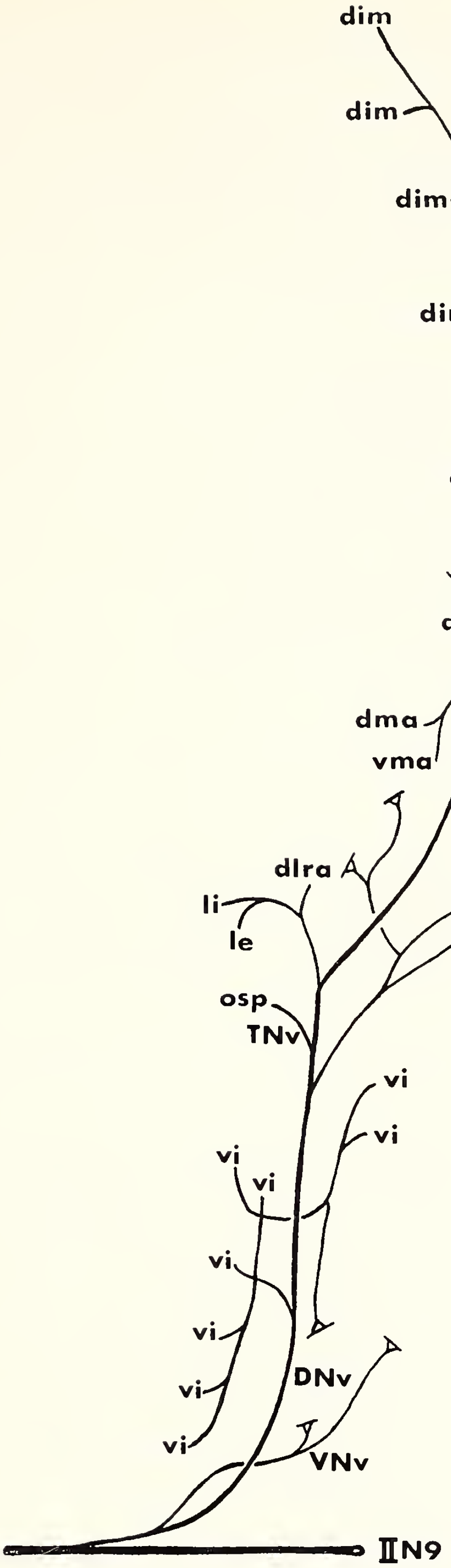

Fig. 13. Diagram of the nerve pattern of the right side of the fourth abdominal segment of the male of *Tibicen chloromera* (Walker) viewed mesally.

Carlet (1876), Vogel (1923), and Myers (1928) have established that this sclerotized V-shaped structure is a modification of the first abdominal sternum. A sternal canal is present within the base of this structure and provides a passageway for two pairs of nerves, IIN8 and IIN9. The "wings" or "arms"

TABLE 8. Musculature of the sound mechanism of *Tibicen chloromera* (Walker).

Muscle	Muscle number	Origin (or attachment)	Insertion (or attachment)
Dorsal muscle	89	Anterior intersegmental fold	Tergal ridge
Dorsal muscle	90	Tergal ridge	Posterior intersegmental fold
Ventral muscle	91	Metafurca	Anterior edge of first abdominal sternite
Ventral muscle	92	Metafurca	Lateral apodemal arm of anterior edge of sternum
Ventral muscle	93	Posterior edge of first abdominal sternum	Posterior intersegmental fold
Tergo-sternal muscle (Tymbal muscles)	94	Basal portion of first abdominal sternum	Terminal plate which attaches to tymbal by a tendon
Tergo-sternal muscle	95	Anterolateral edge of tergum	Lateral apodemal arm of anterior edge of sternum
Tergo-sternal muscle	96	Anterolateral edge of tergum ventrad to 95	Lateral apodemal arm of anterior edge of sternum
Tergo-sternal muscle	97	Anterolateral edge of tergum ventrad to 96	Lateral apodemal arm of anterior edge of sternum
Tergo-sternal muscle	98	Anteroventral edge of tymbal	Lateral apodemal arm of anterior edge of sternum
Tergo-sternal muscle	99	Tergum along lateral edge of mirror	Lateral apodemal arm of posterior edge of sternum
Tergo-sternal muscle	100	Posterior intersegmental fold	Lateral apodemal arm of posterior edge of sternum
Occlusor of spiracle	101	Lateral apodemal arm of posterior edge of sternum	Ventral end of spiracle
Occlusor of spiracle	102	Lateral apodemal arm of posterior edge of sternum	Base of spiracle

of the sclerotized V-shaped structure attach to the tergal ridge of the first abdominal segment.

A comparison of the musculature of the sound mechanism of *Tibicen chloromera* with *Huechys sanguinea* var. *philaemata* described by Maki (1938) and *Cicada* (= *Tibicen*) *plebeia* described by Berlese (1909) is presented in Table 9. The musculature of *Tibicen* differs from that found in the two other species of cicadas compared in Table 9 by the presence of tergo-sternal muscles 96, 97, and 98. Maki's ventral muscle 76 in *Huechys* was not described by Berlese (1909) in *Cicada* (= *Tibicen*) *plebeia*; however, it is present in *Tibicen chloromera*. In *Tibicen*, the dorsal muscles 89 and 90 have attachments on the tergal ridge (tr) of the first abdominal segment (Fig. 2). Berlese (1909) shows in his figure 542 similar points of attachments for the dorsal muscles 37 and 28–29 in *Cicada* (= *Tibicen*) *plebeia*. However, the dorsal muscle 74 of *Huechys sanguinea* var. *philaemata*, as shown by Maki (1938) in his figure 24, has its attachment on the anterior and posterior intersegmental folds of the first abdominal segment.

Innervation of the Sound Mechanism: The innervation of the sound mechanism is shown in Fig. 10. Nerves IIN7, IIN8, and IIN10 + IIN11 provide innervation to the muscles of the first abdominal segment which contains the sound mechanism. Nerve IIN7 issues from the posterior portion of the thoracic–abdominal ganglionic mass and proceeds posteriorly and passes over the mesofurca. Nerve IIN7 receives a nerve branch from the IIN10 + IIN11 nerve before forming the nerve branch IIN7a. Branch IIN7a provides innervation to the ventral muscle 92, the membranous sac of the abdominal air chamber, and occlusor muscle of the first abdominal spiracle 101 before coalescing with the dorsal nerve IIN7. Nerve IIN7 is the anterior dorsal nerve of the first abdominal segment since it terminates in the dorsal muscles 89. Nerve IIN7 provides a nerve branch to the ventral muscle 91 and passes under muscle 91, around the posterior arm of the metafurca, and continues along the anterior edge of the first abdominal segment. Nerve IIN7 provides a sensory nerve branch to the integument and coalesces with nerve IIN10 + IIN11 before innervating the tergo-sternal muscles 95, 96, and 97. Nerve IIN7 then provides a nerve branch to the membranous sac surrounding the tymbal muscle 94 and coalesces with nerve branch IIN7a before providing a nerve branch to the tergo-sternal muscle 98 and dorsal muscle 89 (Fig. 10).

Nerve IIN8 issues from the posterior portion of the thoracic–abdominal ganglionic mass and proceeds posteriorly over the mesofurca. Nerve IIN8 then divides into a dorsal nerve branch IIN8a which terminates in the tergo-sternal muscle 94, and a ventral nerve IIN8 which passes between the ventral muscles 91 and enters the sternal canal. Nerve branch IIN8a is the auditory nerve and proceeds dorsally and for a portion of its length adheres to the IIN8a nerve from the opposite side. Nerve branch IIN8a then receives a nerve branch from the IIN10 + IIN11 nerve and proceeds in a dorso-oblique path over the mesal surface of the large tergo-sternal muscle 94. Nerve IIN8a then passes around the dorso-posterior edge of muscle 94 and enters this muscle along its lateral surface. Nerve IIN8 passes through the sternal canal and provides nerve branches to the integument and ventral muscle 93. Nerve IIN8 then passes along the posterior edge of the first abdominal segment and provides nerve branches to the occlusor muscle of the spiracle 102, tergo-sternal muscles 99 and 100, and the dorsal muscle 90. Nerve IIN8 is the posterior dorsal nerve since it terminates in the dorsal muscle 90 located in the posterior portion of the first abdominal segment.

The IIN10 + IIN11 nerve enters the first abdominal segment after supplying a nerve branch to nerve IIN7 and proceeds posteriorly in a dorso-oblique path and provides a nerve branch which coalesces with nerve IIN8a. The IIN10 + IIN11 nerve continues dorsolaterally and provides a short nerve branch to the tymbal muscle 94 before it loops in an anterior direction and coalesces with nerve IIN7 (Fig. 10). The IIN10 + IIN11 nerve is the sympathetic nerve of Voskresenskaya and Svidersky (1960), who report that without the innervation of the sympathetic nerve the sound-producing system cannot function normally. Therefore, both the auditory nerve, IIN8a, and the sympathetic unpaired nerve,

Table 9. Comparison of the musculature of the sound mechanism of *Tibicen chloromera*, with *Huechys sanguinea* var. *philaemata* (Maki, 1938) and *Cicada* (= *Tibicen*) *plebeia* (Berlese, 1909).

Muscles	*Tibicen chloromera*	*Huechys sanguinea* var. *philaemata* (Maki, 1938)	*Cicada* (= *Tibicen*) *plebeia* (Berlese, 1909)
Dorsal muscles	89	–	37
Dorsal muscles	90	–	28–29
Dorsal muscle	–	74	–
Ventral muscle	91	75	35
Ventral muscle	92	76	–
Ventral muscle	93	–	14 + 15
Tergo-sternal muscle	94	77	XXVI
Tergo-sternal muscle	95	78	–
Tergo-sternal muscle	96	–	–
Tergo-sternal muscle	97	–	–
Tergo-sternal muscle	98	–	–
Tergo-sternal muscle	99	–	XVII
Tergo-sternal muscle	100	83	XVII
First interpleural muscle	–	–	LIII
Occlusor of spiracle	101	79	–
Occlusor of spiracle	102	85	–

IIN10 + IIN11, are necessary for the rhythmic "singing" of the cicada. It is interesting to note that Hagiwara and Watanabe (1956) concluded that the paired tymbal muscles receive alternate impulses from the ganglion, and this alternate activity of the two tymbals may give a double sound vibration frequency.

5. THE MUSCULATURE AND INNERVATION OF THE FOURTH ABDOMINAL SEGMENT

General: The abdominal musculature of adult and larval insects conforms to a simple fundamental pattern which is repeated with only minor variations in each of the pregenital segments (Snodgrass, 1935). The major groups of abdominal muscles found in insects are the dorsal muscles, ventral muscles, lateral muscles, transverse muscles, and spiracular muscles. The dorsal and ventral muscles in most insects occur in two layers and thereby form dorsal internal and external muscles and ventral internal and external muscles. In the male of *Tibicen chloromera* (Walker) the dorsal external and ventral external muscles are absent. The writer observed a similar condition in all of the typical pregenital abdominal segments. Another common form of diversification affecting dorsal and ventral muscles includes a more or less distinguishable grouping of the muscles into median and lateral sets (Snodgrass, 1935). In *Tibicen* the dorsal muscles can be classified into dorsal internal median and dorsal internal lateral muscle groups; however, the ventral internal muscles cannot be classified into median and lateral sets since there are no ventral transverse muscles or a wide separation between the ventral internal muscles.

The musculature of the fourth abdominal segment of the male of the annual cicada, *Tibicen chloromera* (Walker) is shown in Figs. 11 and 12 and a list of the muscles with their muscle numbers and attachments is presented in Table 10.

The innervation of the abdominal musculature with the exception of the muscles of the first abdominal segment is achieved by nerves IIN9. The IIN9 nerves provide a pair of lateral nerve branches to each consecutive pregenital abdominal segment. Figs. 11 and 12 show the innervation of the fourth abdominal segment.

The Musculature of the Fourth Abdominal Segment: The musculature of the fourth abdominal segment of the male of *Tibicen chloromera* (Walker) can be classified into dorsal, ventral, lateral, and spiracular muscles (Table 10). The dorsal muscles are subdivided into dorsal internal median (103) and dorsal internal lateral (104) muscles, dorsal (105) and ventral (106) muscles of the apodeme, and dorsal transverse muscles (107). The dorsal internal median and dorsal internal lateral muscles have their attachments on the anterior and posterior intersegmental folds while the dorsal and ventral muscles of the apodeme have their attachments on the anterior edge of the apodeme and the posterior intersegmental fold. It is interesting to note that there is a complete absence of dorsal external muscles in the pregenital abdominal segments. The usual location of the dorsal external muscles is the posterior portion of the abdominal segment with their attachments on the posterior margin of the tergum and the posterior intersegmental fold. In this position the dorsal external muscles serve as protractors of the abdomen. It appears that the protraction of the abdomen in *Tibicen* is achieved by the contraction of the dorsal and ventral muscles of the tergal apodeme. The dorsal transverse muscle, 107, has its attachments along the lateral edge of the dorsal vessel and the anterolateral intersegmental fold of the tergum.

Eight closely associated sets of ventral internal muscles, 108, are present in *Tibicen*. The ventral internal muscles cannot be grouped into specific median and lateral muscle sets.

Four pairs of lateral muscles are present in *Tibicen*: lateral internal 109, lateral external 110, lateral intrasegmental 111, and the dilator of the abdomen 112 (Figs. 11 and 12). The lateral internal and external muscles are tergo-sternal muscles and have their attachments on the anterior intersegmental fold of the tergum and the internal surface of the anterior sternal apodeme. The lateral intrasegmental muscle is tergo-sternal in its attachments and is located in the posterior portion of the segment. The dilator of the abdomen is attached to the anterolateral edge of the tergum and the external surface of the anterior sternal apodeme.

The spiracle of the fourth abdominal segment is located in the anterolateral corner of the sternum. The occlusor muscle of the spiracle has its attachments on the anterolateral portion of the sternum adjacent to the sternal apodeme and to the ventral edge of the spiracle.

Maki (1938) in his figure 24 shows the musculature of the third abdominal segment of *Huechys sanguinea* var. *philaemata.* The musculature of the fourth abdominal segment of *Tibicen chloromera* (Walker) is homologous to the third segment of *Huechys sanguinea* var. *philaemata* with the exception of the dorsal internal lateral muscles 104, the lateral intrasegmental muscle 111, and the dilator of the abdomen 112 of *Tibicen* (Table 11).

The Innervation of the Fourth Abdominal Segment: The innervation of the fourth abdominal segment is achieved by a pair of lateral nerve branches which arise from the IIN9 nerves. The IIN9 nerves issue from the posterior end of the thoracic–abdominal ganglionic mass and pass over the mesofurca and metafurca and between the ventral muscles into the sternal canal. After the IIN9 nerves pass through the sternal canal they provide a pair of lateral nerve branches to the second and remaining pregenital abdominal segments. The lateral nerve branch from nerve IIN9 divides into a dorsal nerve and ventral nerve prior to passing under the ventral internal muscles of the fourth abdominal segment. The innervation of the fourth abdominal segment is shown in Figs. 11 and 12. The ventral nerve (VNv) passes under the dorsal nerve (DNv) and terminates in the integument beneath the ventral internal muscles 108 (Fig. 12). The dorsal nerve provides a nerve branch to the ventral internal muscles which are innervated along their external surface.

The dorsal nerve proceeds laterally and provides a nerve (TNv) to the occlusor muscle of the spiracle 113 (Fig. 13). Case (1957) presents experimental evidence that the median and transverse nerves provide a neural pathway connecting the spiracular mechanism with the central nervous system. Schmitt (1965) presents a comparative morphological study on the transverse nerves in the abdominal nervous system of insects and concludes that, in insects which apparently lack median and transverse nerves, these nerves have become incorporated in the longitudinal connectives and lateral segmental nerves. In the majority of insects reviewed by Schmitt, the transverse nerve also innervates the alary muscles. In *Tibicen chloromera* (Walker) the writer could not determine the innervation of the alary muscles; however, it appears reasonable to conclude that the innervation of the occlusor muscle of the spiracle of *Tibicen* is accomplished by fibers of the transverse nerve which have become incorporated in the dorsal nerve.

After providing a nerve branch to the occlusor muscle of the spiracle, the dorsal nerve ramifies into three nerve branches. The anterior nerve branch innervates the lateral internal muscle 109, lateral external muscle 110, and the dilator of the abdomen 112. The posterior nerve branch divides into a sensory nerve which terminates in the integument and a nerve branch which innervates the lateral intrasegmental muscle 111 (Figs. 11 and 12).

TABLE 10. The musculature of the fourth abdominal segment of *Tibicen chloromera* (Walker).

Muscle	Muscle number	Origin (or attachment)	Insertion (or attachment)
Dorsal muscles			
Dorsal internal median muscles	103	Anterior intersegmental fold	Posterior intersegmental fold
Dorsal internal lateral muscles	104	Anterior intersegmental fold	Posterior intersegmental fold
Dorsal muscle of apodeme	105	Anterior edge of tergal apodeme	Posterior intersegmental fold
Ventral muscle of apodeme	106	Anterior edge of tergal apodeme	Posterior intersegmental fold
Dorsal transverse muscle	107	Anterior intersegmental fold	Lateral edge of the dorsal vessel
Ventral muscles			
Ventral internal muscles	108	Anterior intersegmental fold	Posterior intersegmental fold
Lateral muscles			
Lateral internal muscle	109	Anterior intersegmental fold of tergum	Internal surface of sternal apodeme
Lateral external muscle	110	Anterior intersegmental fold of tergum	Internal surface of sternal apodeme
Lateral intrasegmental muscle	111	Posterolateral portion of tergum	Lateral edge of sternum
Dilator of the abdomen	112	Lateral edge of tergum	External surface of sternal apodeme
Muscles of the spiracle			
Occlusor	113	Anterolateral portion of sternum adjacent to the sternal apodeme.	Ventral edge of spiracle

The dorsal nerve proceeds dorsally in an oblique-posterior direction over the tergal apodeme and supplies a nerve branch to the dorsal and ventral muscles (104 and 105) of the apodeme (Figs. 11 and 12). The dorsal nerve continues dorsally along the posterior portion of the tergum and passes over the dorsal internal lateral muscles 104 and provides nerve branches to these muscles. The dorsal nerve then divides into three nerve branches; two nerve branches pass laterally under the dorsal internal median muscles and terminate in the integument while the dorsal nerve passes mesally over the dorsal internal median muscles supplying these muscles with nerve branches. The dorsal nerve terminates in the first set of dorsal internal median muscles (Fig. 11).

The segmental nerve pattern in the male cicada, *Tibicen chloromera* (Walker), is notably abbreviated when compared to the innervation pattern of some families of Orthoptera, as described by Schmitt (1954), *Chauliodes formosanus* as described by Maki (1936), the larva and adult of *Hyalophora cecropa* as described by Libby (1959 and 1961), and in *Pteronarchys* as described by Schmitt (1963). The abbreviated nerve pattern in *Tibicen* is largely due to the absence of the dorsal and ventral external muscles and by the condensation

Table 11. A comparison of the musculature of the fourth abdominal segment of *Tibicen chloromera* (Walker) to the musculature of the third abdominal segment of *Huechys sanguinea* var. *philaemata* described by Maki (1938).

Muscle groups	*Tibicen chloromera*	*Huechys sanguinea* var. *philaemata* (Maki, 1938)
Dorsal muscles		
Dorsal internal median muscles	103	86
Dorsal internal lateral muscles	104	–
Dorsal muscle of apodeme	105	87
Ventral muscle of apodeme	106	88
Dorsal transverse muscle	107	89
Ventral muscles		
Ventral internal muscles	108	90
Lateral muscles		
Lateral internal muscle	109	91
Lateral external muscle	110	92
Lateral intrasegmental muscle	111	–
Dilator of the abdomen	112	–
Muscles of the spiracle		
Occlusors of the spiracle	113	93

of the ventral nerve cord which has resulted in the formation of a thoracic–abdominal ganglionic mass located in the mesothorax. With the condensation of the ventral nerve cord, the motor axons which supply the innervation to the typical pregenital abdominal segments have become incorporated within a single pair of nerves, IIN9. The IIN9 nerves supply a pair of lateral nerve branches to each consecutive abdominal segment after which there are no nerve connections between segments.

The innervation pattern of the fourth abdominal segment of *Tibicen* is shown in Fig. 13. The dorsal nerve supplies innervation to the dorsal and ventral internal longitudinal muscles which are considered primitive muscle groups of the segmental musculature and are therefore useful in the establishment of a criteria of nerve homology. Schmitt (1954) shows that the dorsal and ventral internal muscles of *Dissosteira*, *Acheta*, and *Periplaneta* are innervated by nerve branches from the dorsal nerve. Libby (1959 and 1961) shows a similar innervation of the same muscle groups in the larva and adult of *Hyalophora*.

Further investigations of insects possessing a thoracic–abdominal ganglionic mass located in the thorax must be conducted before significant comparisons can be made with the segmental nerve pattern of *Tibicen*.

SUMMARY AND CONCLUSIONS

The musculature and innervation of the thorax, of the sound mechanism, and of a typical pregenital abdominal segment of the male of the annual cicada, *Tibicen chloromera* (Walker) are described. The musculature of the thorax and abdominal segments of *Tibicen* is essentially homologous to the musculature of the male cicada *Heuchys sanguinea* var. *philaemata* as described by Maki (1938).

The ventral nerve cord consists of a subesophageal ganglion, prothoracic ganglion, and a thoracic–abdominal ganglionic mass. There are no ganglia present in any of the abdominal segments. The abdominal segments are innervated by lateral nerve branches arising from a pair of nerves that originate from the posterior portion of the thoracic–abdominal ganglionic mass located in the mesothorax. Eight pairs of nerves arise from the subesophageal ganglion and supply innervation to the muscles associated with the feeding apparatus, the salivary glands, the lateral ducts of the salivary glands, and some of the muscles of the cervical area.

The prothoracic ganglion and the anterior portion of the thoracic–abdominal ganglionic mass are covered dorsally by ventral muscles. The prothoracic ganglion supplies innervation to some of the muscles of the cervical area and the muscles of the prothorax. The thoracic–abdominal ganglionic mass provides innervation to the posterior tergo-sternal muscles of the prothorax, the muscles of the mesothorax, metathorax, and all the abdominal segments. No median nerves are visible between the subesophageal ganglion, prothoracic ganglion, and the thoracic–abdominal ganglionic mass. However, the median nerves are probably included within the interganglionic connectives. Spiracular muscles of the thoracic segments are innervated by nerves which arise from the dorsolateral area of the prothoracic ganglion and the thoracic–abdominal ganglionic mass. The nerves to the spiracular muscles are apparently the transverse nerves of the "ventral sympathetic nervous system."

The sound mechanism is contained within the first abdominal segment. An invagination of the first abdominal sternite serves as an area for attachment and support for the large tymbal muscles. A sternal canal is located within the sternal invagination and permits the passage of two pairs of nerves. One pair of nerves innervates the muscles in the posterior portion of the first abdominal segment while the remaining pair of nerves provides innervation to the remaining abdominal segments.

Each typical pregenital abdominal segment is innervated by a pair of lateral nerve branches which arises from a single pair of nerves originating from the posterior end of the thoracic–abdominal ganglionic mass and pass through the sternal canal. There are no nerve connections between the typical pregenital abdominal segments once the lateral nerves enter their respective segments. A single nerve branch from the dorsal nerve innervates the occlusor muscle of the spiracle of the fourth abdominal segment. It appears that the innervation of the occlusor muscle of the spiracle is achieved by fibers of the transverse nerve which have become incorporated in the lateral nerve branches to the abdominal segments.

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ABBREVIATIONS USED ON THE FIGURES

AT—Anterior tentorial arm
AWN—Anterior wing nerve
Ba_3—Metathoracic basalare
bp—Bristle plate
CoeCon—Circumesophageal connective
Con—Connective
Cv—Cervix
cv—Cervical sclerite
Cx_1—Coxa of the prothoracic leg
Cx_2—Coxa of the mesothoracic leg
Cx_3—Coxa of the metathoracic leg

dil—Dorsal internal lateral muscle
dim—Dorsal internal median muscle
dlra—Dilator muscle of the abdomen
dlSyr—Dilator muscle of the salivary syringe
dma—Dorsal muscle of the tergal apodeme
DNv—Dorsal nerve
Fu$_2$—Mesofurca
Fu$_3$—Metafurca
GI—Prothoracic ganglion
GII—Thoracic–abdominal ganglionic mass
L—Leg
Lb—Labium
le—Lateral external muscle
li—Lateral internal muscle
lis—Lateral intrasegmental muscle
LmNv—Labral nerve
M—Mirror of the sound mechanism
mlb—Muscles of labium
mr—Muscles of the rod
MS—Membranous sac of the sound mechanism
mxb—Maxillary bristle
Op—Operculum
osp—Occlusor muscle of the spiracle
pl—Tymbal muscle plate
PlA$_1$—Prothoracic pleural arm
PlA$_2$—Mesothoracic pleural arm
PlA$_3$—Metathoracic pleural arm
pmdb—Protractor muscle of the mandibular bristle
PT—Posterior tentorial arm
PWN—Posterior wing nerve
r—Rod
rmdb—Retractor muscle of the mandibular bristle
rmxb$_1$—Internal retractor muscle of the maxillary bristle
rmxb$_2$—External retractor muscle of the maxillary bristle
Sa$_2$—Subalare of the mesothorax
Sa$_3$—Subalare of the metathorax
SLD—Salivary duct
SLGL—Salivary gland
SoeGng—Subesophageal ganglion
Sp$_2$—Mesothoracic spiracle
Sp$_3$—Metathoracic spiracle
sp—Fourth abdominal spiracle
T$_1$—Prothoracic tergum
T$_2$—Mesothoracic tergum
T$_3$—Metathoracic tergum
tapd—Tergal apodeme
TB—Tentorial bridge
tg—Tegula
tn—Tendon between tymbal plate and tymbal
TNv—Transverse nerve

Tr—Trachea
tr—Tergal ridge
TYM—Tymbal
Vi—Ventral internal muscles
Vma—Ventral muscle of the tergal apodeme
Vnv—Ventral nerve
wg—Wing of sclerotized V-shaped structure of first abdominal segment
1Ph—First phragma
2Ph—Second phragma
I—First abdominal segment
ISp—First abdominal spiracle
II—Second abdominal segment
1pmxb—Protractor muscle of the maxillary bristle
2pmxb—Protractor muscle of the maxillary bristle

Spiders from Powdermill Nature Reserve

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Abstract: This paper is a list of 150 species of spiders collected during a 2-week study of the fauna of Powdermill Nature Reserve in Pennsylvania.

Local and regional faunal lists are the backbone of ecological and zoogeographical studies. Such lists provide the detailed information on local faunas necessary for syntheses of a broader scope. The spider fauna of Pennsylvania has been sadly neglected. Distribution maps in recent taxonomic revisions almost invariably show a lack of locality records from this state. There has been only one list of Pennsylvania spiders published during the last half century (Truman, 1942): a list of spiders from Presque Isle, Erie County. This present paper is also a local faunal list.

The Powdermill Nature Reserve of Carnegie Museum is an area of about 1,500 acres in the Ligonier Valley of Westmoreland County, Pennsylvania. The reserve includes a variety of woodland and open (chiefly old field) habitats. This collection was primarily made during a 2-week study in June and July, 1965, with a few additional specimens collected at other times of the year. This list must, of necessity, be regarded as preliminary. With the exception of duplicates retained by the author, the specimens are deposited in Carnegie Museum.

The collection consists of over 1,000 specimens of mature spiders, representing about 150 species. The list from Presque Isle also includes about 150 species, but the two lists have only half their species in common. These lists, along with scattered reports, bring the published number of Pennsylvania species between 200 and 250. Judging by the fauna of New York state, there should eventually be more than 500 species of Pennsylvania spiders.